ECOLOGY

Vol. 36 OCTOBER, 1955 No. 4

ANALYSIS OF PHYTOPLANKTON YIELDS IN RELATION TO CERTAIN PHYSICAL AND CHEMICAL FACTORS OF LAKE MICHIGAN

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INTRODUCTION

It is known that the plankton production of a given body of water changes from year to year and from season to season. Many data, both qualitative and quantitative, have accumulated during the last 20 years (see McCombie 1953, Pennak 1946, and Welch 1935, for bibliographies) on plankton productivity of fresh-water areas.

Many workers (see Damann 1941 for a review of the literature) have studied the plankton of Lake Michigan. Quantitative analysis of the shore phytoplankton at Evanston was initiated by Daily (1938), who secured data on temperature, sunlight, turbidity, bacteria, and phytoplankton. Damann (1941) continued the study begun by Daily. Neither of these studies included chemical factors. Damann (1943) examined monthly chemical determinations (1926-1927) from the Water Purification Division of Chicago and concluded that chemical factors were not the determining factors of plankton seasonal periodicity.

The present study contains data obtained from the shore waters of Lake Michigan at Evanston, during the collecting year of April, 1953, through March, 1954. A quantitative analysis has been made of the phytoplankton production during this period and compared with the data of 1938 to 1945. Also a study has been made of certain physical and chemical factors which may have a direct or indirect relationship to the phytoplankton production. A further study should be made not only on chemical factors not included in this study, but also on seston determinations and light penetration.

The author wishes to express her sincere appreciation to Professor L. H. Tiffany for his most willing help and guidance, and particularly for the identification of some doubtful phytoplankton genera. Thanks are also due Professor R. O. Freeland for suggestions regarding apparatus and techniques.

MATERIALS AND METHODS

With varying intervals between successive collections, samples were taken for a complete year, April, 1953, to April, 1954. On October 20, 21, and 22, collections were made continuously every 6 hours. Collections were made from the end of the breakwater just south of Cresap Laboratory on the Northwestern University Campus. This breakwater extends about 65 meters into Lake Michigan and the depth of the water at the collecting station is approximately 2 meters. Samples were taken from the surface and the bottom. Since there was no appreciable difference, however, in the vertical distribution of phytoplankton nor of the physical and chemical factors of the water in the 2 samplings; only surface samples are contained in these data. Samples were also obtained in the day and night of the same 24-hour period and no marked differences occurred unless there had been a definite change in the condition of the water such as that caused by a storm. Only the data of one collection per specific day are reported with the exception of some collections in October which were taken every 6 hours for 2 days.

Temperature readings were taken with a Fisher maximum-minimum thermometer suspended in the water. A record of pH was maintained for some time but was discontinued in a few months since the water varied only from pH 8.25 to 8.48.

Estimates of turbidity were made at each collection time by observation of color of water and amount of inorganic and organic material in the concentrates.

Collections for phytoplankton enumeration and chemical analysis were secured with a 2-liter Foerst Improved Water Sampler. Dissolved oxygen, free carbon dioxide, carbonate and bicarbonate values were obtained by use of the methods stated in Welch (1948). The per cent saturation of oxygen was obtained by the use of Rawson's nomogram (Rawson 1944).

One liter of the water was centrifuged with a Foerst continuous-flow centrifuge. The concentrate was transferred to vials and diluted to 10 c.c. or more, according to the turbidity of the sample; this was then preserved with 4 per cent formalin. The phytoplankters were counted with a Sedgewick-Rafter cell and a Whipple micrometer in a binocular microscope. At least 2 one c.c. samples of the concentrate were used and by counting 10 fields in the counting chamber the number of phytoplankters per milliliter of unconcentrated lake water was estimated. The counting units of phytoplankton were those values assigned by Wright and Tidd (1933).

Results and Discussion

Physical Data

Temperature.—Temperature readings were taken at the time of each collection. These are shown in Fig. 1. Usually there was no difference between the temperature of the surface and bottom, and only the surface temperatures are recorded here. If a difference was noted, it was less than 1°C. with the exception of one collection

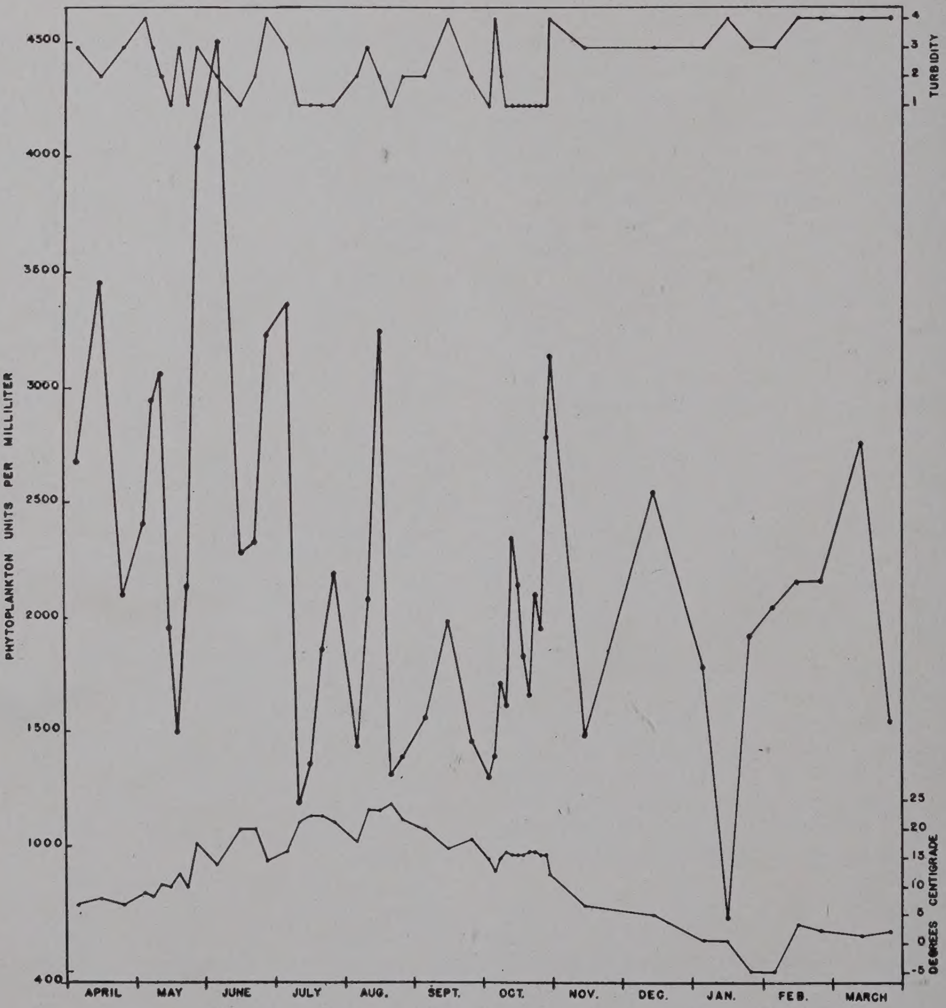

Fig. 1. Graphs showing the yields of total phytoplankton in units per milliliter; the temperature in degrees centigrade; and the turbidity indexed as: 1—very low; 2—low to medium; 3—relatively high; 4—very high.

in May which had a difference of 2°; no chemical differences were observed in this particular collection.

The temperature curve, when compared with the curve of the total phytoplankton yield (Fig. 1) does not appear to substantiate the conclusion of Damann (1941) that temperature has a pronounced effect upon total phytoplankton production. Damann (1943) stated that the diatoms, except *Tabellaria* and *Fragilaria,* and the green algae seem to be consistently inhibited by a water temperature of approximately 60°F. In this same study he also indicated that *Asterionella* usually increased with an increase in water temperature up to approximately 60°F; above this value the yield is reduced. The critical temperature for *Synedra* seemed to be slightly lower than that of *Asterionella.*

The data of this present study do not support these conclusions. The Chrysophyta mean for the collecting year was 638 units per ml. On 7 occasions the water temperature ranged from 61°F. to 74°F. and the Chrysophyta ranged from 824 to 1979 units per ml. The *Asterionella* mean was 36 units per ml. and counts were made of 133, 67, and 123 units per ml. when the temperatures were

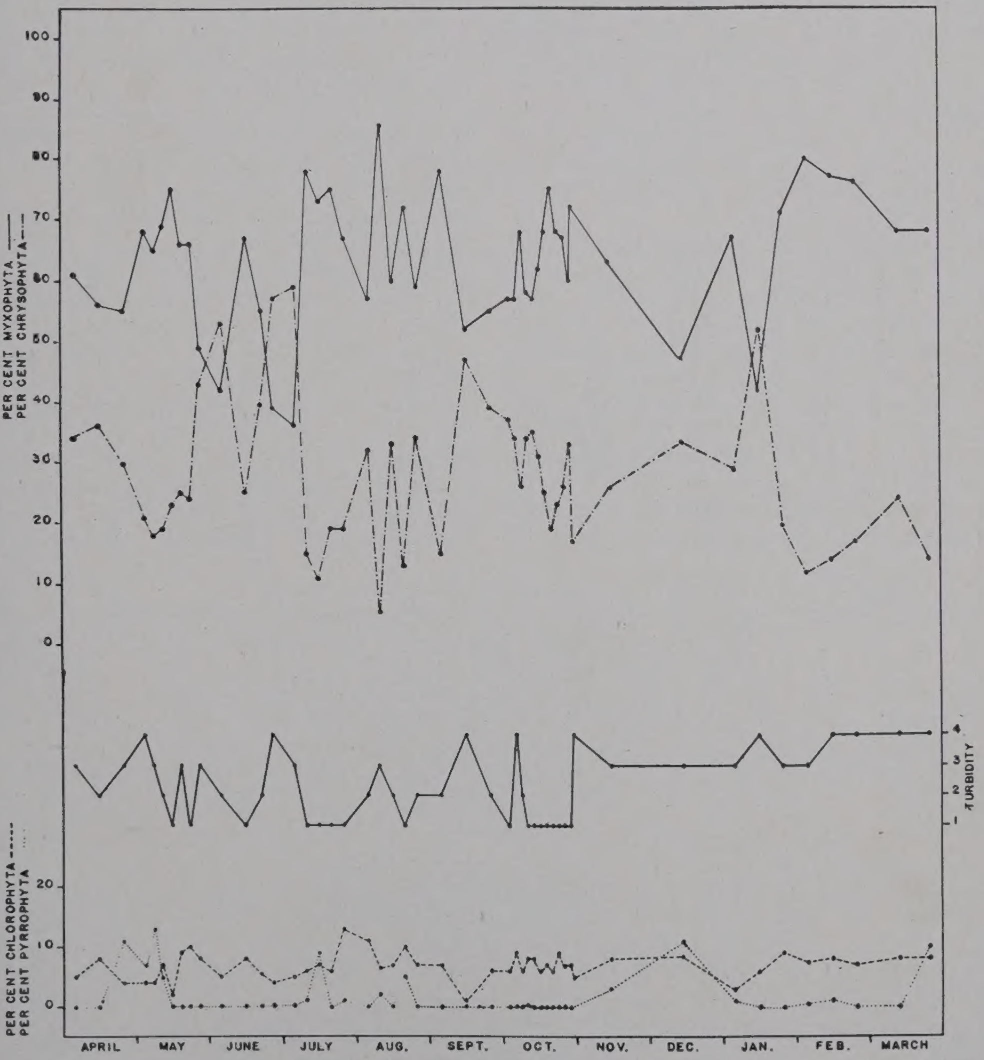

Fig. 2. Graphs showing the turbidity and the per cent of each phylum found in each collection of phytoplankton.

respectively 64, 68, and 61°F. The *Synedra* mean was 240 units per ml. and on 7 occasions *Synedra* ranged from 270 to 916 units per ml. with the temperature ranging from 62 to 68°F. The Chlorophyta mean was 145 units per ml. and on 8 occasions counts ranged from 158 to 325 units per ml. with a temperature range of 61 to 74°F.

The temperature range noted above apparently is not directly correlated with the productivity of any phylum and its effects must be considered in relation to the many other environmental factors which influence phytoplankton production.

Turbidity.—Turbidity values were roughly indexed according to the color of the lake and the amount of material in the concentrated sample. The graph in Fig. 1 is based upon the following assigned values: 1—very low; 2—low to medium; 3—relatively high; 4—very high. Most of the suspended matter was inorganic and settled quickly. The great turbidity of the shore waters of Lake Michigan, much of the time, is due to heavy wind and wave action plus strong undertow currents.

When these data are compared with the total phytoplankton yield, no consistent trend is apparent. It should be noted (Fig. 2) that whenever the Myxophyta were 70 per cent or more of the population total, the turbidity index was 1 or 2, with the exceptions of the January 19 and February collections. The Chrysophyta populations which were 40 per cent or more of the total had an index of 3 or 4 with the exception of the June 3 collection which had an index of 2. Although the Chlorophyta populations were small, the data indicate a general increase in population when the turbidity is low and a corresponding decrease when the turbidity is higher.

The author agrees with Daily (1938) and Chandler (1940) that it is difficult to make definite statements about the effects of turbidity upon plankton pulses. From the data presented in this paper it appears that a period of high turbidity does precede a hgh plankton pulse and that during the pulse, the turbidity is relatively low. The data indicate 2 exceptions to this generalization; in June and October over 3,000 units per ml. of phytoplankton were collected when the turbidity was indexed at 4. Harris and Silvey (1940) found in their work on reservoir lakes of Texas that some lakes had maximum plankton production during low turbidity periods and that others had maximum plankton production during high turbidity periods.

Dissolved oxygen.—As Table I indicates, the dissolved oxygen was highest in April, 1953, and March, 1954, with peaks of 12.6 p.p.m. The tension gradually decreased to 4.6 p.p.m. on the 29th of August. The tension then increased until the 22nd of October for a high of 11.0 p.p.m. The tension varied considerably during the winter months; the lowest oxygen tension value obtained, 3.3 p.p.m. was on December 5.

There appears to be no correlation between the oxygen saturation curve and that of the total phytoplankton. Nor is there any apparent correlation of the saturation curve and the individual productivity curves of phyla. There does appear to be a tendency for higher saturation values when turbidities are low; however, the data do not show a consistent relationship. Since dissolved

TABLE I. *Chemical data for each plankton collection*

	4-21-53	4-23-53	4-28-53	5-1-53	5-5-53	5-7-53	5-12-53	5-15-53	5-19-53	5-26-53	6-3-53	6-19-53	6-24-53	6-30-53	7-8-53	7-14-53	7-17-53	7-23-53	7-29-53	8-4-53	8-10-53	8-15-53	8-21-53	8-29-53	9-5-53
Dissolved oxygen p.p.m.	11.8	12.6	12.4	11.2	11.4	10.2	11.8	12.0	12.2	11.6	11.2	9.8	9.2	11.6	10.4	10.4	9.4	8.2	10.4	10.2	8.0	8.6	8.2	4.6	5.2
Oxygen % saturation	96	105	100	97	97	91	104	111	107	120	107	107	100	112	105	116	104	93	116	106	94	100	97	51	56
Free carbon dioxide p.p.m.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phenophthalein alkalinity p.p.m.	8	9	9	9	9	12	8	9	7	13	13	13	11	9	12	14	13	13	12	9	8	4	8	9	9
Methyl orange alkalinity p.p.m.	117	128	123	131	133	126	130	144	132	132	121	115	141	129	121	125	119	122	128	124	132	127	130	121	130
Carbonates p.p.m.	16	18	18	18	18	24	16	18	14	26	26	26	22	18	24	24	26	26	24	18	16	8	16	18	18
Bicarbonates p.p.m.	109	119	114	122	124	114	122	135	125	119	108	112	130	120	109	115	106	109	116	117	124	123	122	112	121

	9-14-53	9-23-53	10-1-53	10-9-53	10-15-53	10-20-53 11:45 A.M.	10-20-53 5:45 P.M.	10-20-53 11:45 P.M.	10-21-53 5:45 A.M.	10-21-53 11:45 A.M.	10-21-53 5:45 P.M.	10-21-53 11:45 P.M.	10-22-53 5:45 A.M.	10-31-53	11-13-53	12-5-53	1-4-54	1-9-54	1-19-54	2-2-54	2-15-54	2-27-54	3-6-54	3-23-54
Dissolved oxygen p.p.m.	6.6	6.2	6.4	6.6	6.6	9.2	9.4	10.2	10.0	10.0	10.4	10.4	11.0	6.6	4.4	3.2	4.2	9.4	6.8	4.8	6.2	8.4	12.6	8.4
Oxygen % saturation	67	65	63	62	64	93	94	102	100	101	104	103	109	61	35	25	29	65	42	30	39	61	89	61
Free carbon dioxide p.p.m.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	1.0	1.0	2.0	6.0	7.0	7.0	14.0
Phenophthalein alkalinity p.p.m.	9	11	7	10	11	9	9	11	14	14	12	12	12	12	10	7	0	0	0	0	0	0	0	0
Methyl orange alkalinity p.p.m.	131	119	124	127	119	113	115	113	112	115	118	116	120	115	117	119	120	128	121	134	95	105	124	128
Carbonates p.p.m.	18	22	14	20	22	18	18	22	28	28	24	24	24	24	20	14	0	0	0	0	0	0	0	0
Bicarbonates p.p.m.	122	108	117	107	108	104	106	102	98	97	106	104	108	103	107	112	120	128	121	134	95	105	124	128

oxygen is largely the result of agitation of the water, a positive correlation between the productivity of phytoplankton and saturation values is not to be expected.

Free carbon dioxide.—Free carbon dioxide did not appear until January 4 (Table I). It remained a constant 1 p.p.m. during that month. In February, it increased to 2, 6, and 7 p.p.m. The last March collection contained 14 p.p.m. Perhaps the heavy ice and snow cover on the shore waters, combined with the low temperatures during January, February, and March prevented the release, to a certain extent, of the carbon dioxide by wave action.

Alkalinity.—As Chandler (1940, 1942, 1944) reported in his work on Lake Erie, the bicarbonates were responsible for most of the alkalinity of the shore waters of Lake Michigan (Table I). Bicarbonate highs of 135 and 134 p.p.m. were reached on May 15 and February 2 respectively; a bicarbonate low of 95 p.p.m. also occurred on February 15. Carbonate highs of 28 p.p.m. occurred in October; none were present from January 4 through March. The methyl orange high,

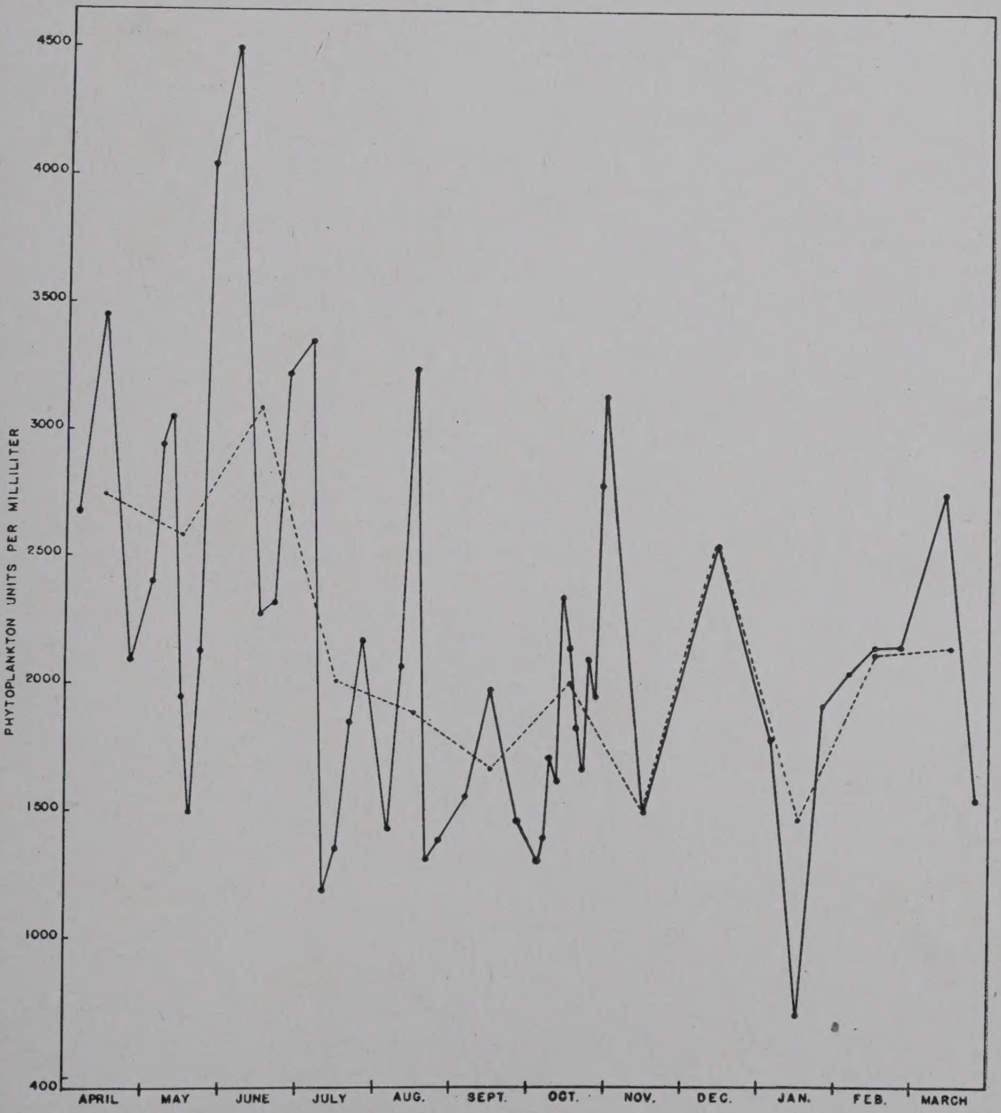

Fig. 3. Graphs showing total phytoplankton yield in units per milliliter for each collection and the phytoplankton monthly averages.

144 p.p.m., occurred on May 15 and the low, 95 p.p.m. on February 15.

Phytoplankton

Total phytoplankton.—The total number of phytoplankton units frequently varied a great deal from one collection time to another. The highest number collected, 4,507 units per ml., was obtained on June 3, 1953. The low of 687 units per ml. was collected on January 9, 1954. According to Pennak (1946), a pulse is that number of organisms which is 2 or more times the annual mean number of organisms. If this definition is used, only one pulse occurred during the entire collecting year. The annual phytoplankton mean was 2,169 units per ml.; therefore, a pulse should contain 4,338 or more phytoplankters. The high previously mentioned then constitutes the pulse. However, as Fig. 3 indicates, 5 minor pulses over 3,000 units per ml. occurred throughout the year. Including the highest pulse, 8 collections contained over 3,000 units per ml.

The collections in November and December probably do not give a true picture of the phytoplankton production since only one collection was taken in each of these months. The monthly averages given also in Fig. 3 indicate clearly that a true picture of the production is not given by the monthly averages. This is especially true if the exact time of a pulse is to be established.

The data of Fig. 3 show a much higher production than did the data of Daily (1938) and Damann (1941) who reported peaks of 3,688 and 1,052 respectively for the periods of May 1937 to May 1938, and November 1938 to November 1939. It would appear that this difference is not due to an extremely high production in 1953-1954, but rather due to the difference in counting technique.

It is difficult to compare the 1953-1954 data with those of Damann (1945) who tabulated the results of 17 collection years of total plankton by the Chicago, Milwaukee, and Michigan City Water Works. The plankters enumerated in his tabulation were collected from cribs that were two to four miles off shore and were also taken from a depth of 15 to 30 feet. It seems logical to assume that organisms found this far off shore and at this depth would be different in kind and also populations. This investigation revealed that the average total plankton population for the 17 years (1926-1942) was a little over 900 organisms per ml. The highest average obtained was 1,277 plankters per ml. in 1942. These two figures are considerably lower than the average annual phytoplankton yield, 2,169 units per ml., determined by this study.

From the data shown in Fig. 3, it is difficult to interpret any seasonal trends or tendencies. Usually large lakes have a bimodal curve with population increases in late spring and fall. Even though these data only indicate a distinct general population increase in the spring for an extended time period, phytoplankton population of Lake Michigan does in all probability, exhibit a bimodal curve. The composition of the algal flora encountered suggests that the shore plankton of Lake Michigan contains a number of adventitious forms and does not give a true picture of the plankton production of the lake as a whole. The shore waters are constantly subjected to changing currents and strong wave action which would have a greater effect on populations in shallow waters than in those in offshore open waters.

During October, an unusual condition of extreme calmness of water existed for a period of more than a week. It seemed feasible to take collections at much shorter time intervals to see if the population picture would produce any trends when the environment was somewhat similar to that of a pond or a body of standing water. As stated earlier in this paper, from October 20 to 22, collections were taken every 6 hours for a 48-hour period. It is unfortunate that the collections were not extended over a longer period since there

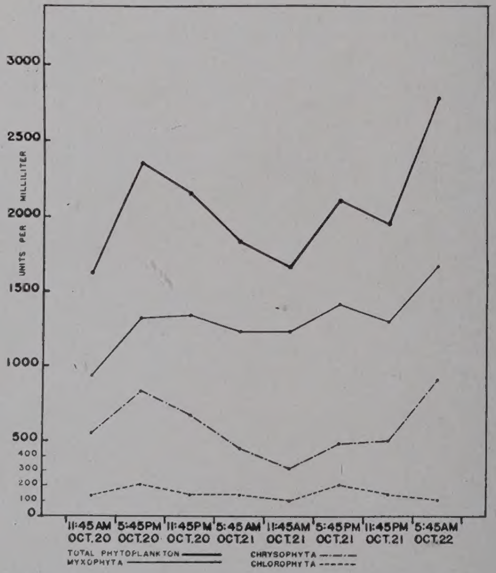

Fig. 4. Graphs showing total phytoplankton yields and phylum yields in units per milliliter during the six-hour collections in October.

seem to be definite peaks established in this short time period. As Fig. 4 indicates the 2 lows were 24 hours apart.

Algal phyla present.—Chlorophyta, Chrysophyta, Myxophyta, and Pyrrophyta were represented in the collections obtained throughout the collecting year. Contrary to the data of Daily (1938) and Damann (1941) who found the diatoms to comprise the bulk of the phytoplankton, the Myxophyta was the predominant phylum. The predominance of this phylum is due to the presence of *Anacystis* in exceedingly high numbers. The numbers of this plankter are, at best, only a rough estimate of the actual population because of the many single-celled units, in part, due to the centrifuge action. These cells are quite small and it is possible for them to have been easily overlooked at the 100 power magnification used by previous workers.

The Chrysophyta were the next greatest in

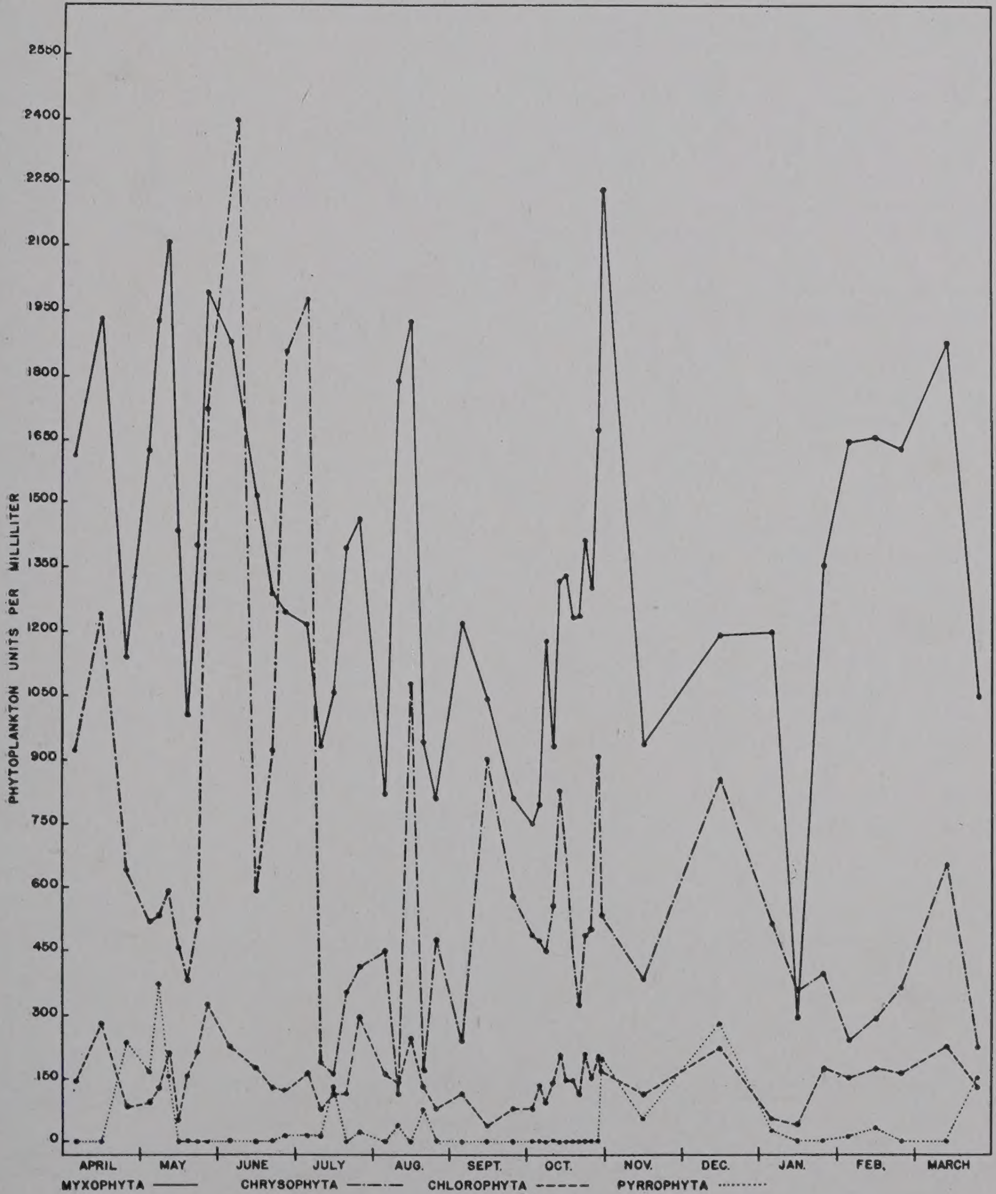

FIG. 5. Graphs showing phylum yields in units per milliliter for each collection.

abundance and then the Chlorophyta with the Pyrrophyta occurring sporadically and in relatively small numbers. Figure 5 shows the total numbers of the various phyla in each collection. In general, the individual peaks of each phylum correlate with the total collection peaks. This is shown more markedly in Figure 4 which indicates the phyla totals during the six-hour collection intervals in October.

The mean number of Chlorophyta for the year was 145 units per ml. If the previously defined pulse is determined on the phylum level, then a Chlorophyta pulse in this study, must attain or exceed a count of 290 units per ml. Two pulses

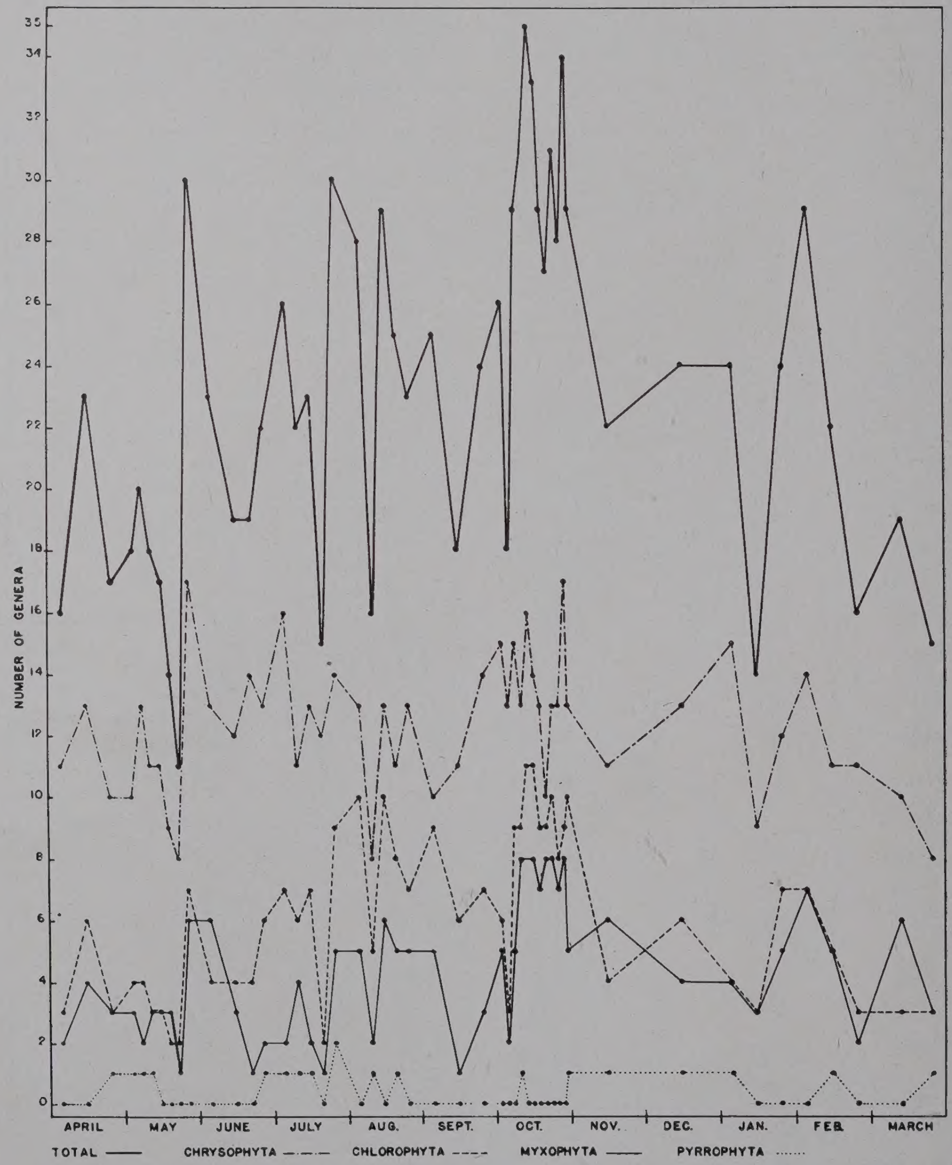

FIG. 6. Graphs showing the total number of genera and the numbers of genera in each phylum for each collection.

did occur on May 26 and July 29 with counts of 325 and 291 units per ml. respectively. The mean number of Chrysophyta was 638 units per ml., and 1,276 units per ml. the pulse number. On May 26 and June 3, highs of 1,719 and 2,400 units per ml. occurred; highs of 1,852 and 1,979 units per ml. again occurred on June 30 and July 8. The Myxophyta mean was 1,342 units per ml. Accordingly, a Myxophyta pulse must then have a count of at least 2,684 units per ml. At no time was this figure reached. The established Pyrrophyta mean was 40 units per ml.; however, this is not a significant figure because of their sporadic appearance.

Figure 2, which indicates the relative per cent of the phyla in each collection, shows a striking correlation between the Myxophyta and Chrysophyta in each collection. It is quite evident that the relative per cent of Myxophyta is inversely proportional to the relative per cent of Chrysophyta. In this respect, these data concur with those of Lake Erie reported by Chandler (1940, 1942, 1944) and Chandler and Weeks (1945).

Algal genera of the plankton.—In an effort to determine whether the number of genera increased or decreased with a corresponding increase or decrease of the total population, Fig. 6 was drawn. From this graph it can be seen that there is a general tendency for the number of genera to increase when the total phytoplankton increases.

Nineteen genera of Chlorophyta appeared throughout the year. Of these, only 3, *Ankistrodesmus, Scenedesmus,* and *Westella* occurred consistently in the collections. Greatest numbers of organisms and genera within the Chlorophyta occurred in the months of July through October.

Twenty-five genera of Chrysophyta occurred throughout the year. The diatoms, *Asterionella, Diatoma, Fragilaria, Melosira, Navicula, Nitzschia, Stephanodiscus* and *Cyclotella, Synedra,* and *Tabellaria,* were present in almost all of the collections and comprise the majority of organisms in the total count of Chrysophyta. There was a tendency for the total numbers to be lower during the summer months. As previously stated, the Myxophyta was the most abundant phylum in numbers of phytoplankton; however, only 15 genera were observed throughout the year. *Anacystis* was responsible for the large numbers of *Myxophyta* and was the only genus represented in every collection. The Pyrrophyta did not appear often in the collections and were represented only by *Ceratium* and *Peridinium.*

SUMMARY

1. Frequent collections of near-shore water of Lake Michigan at the Northwestern University Campus were taken during the year 1953-1954. Data were collected on certain physical and chemical factors in addition to quantitative analysis of phytoplankton.

2. The highest number of organisms, 4,507 units per ml., was obtained in June and the lowest number, 687 units per ml., was obtained in January. The annual phytoplankton mean was 2,169 units per ml. One major pulse occurred in the spring, and 5 minor pulses occurred throughout the year.

3. There was a general tendency for the numbor of genera to increase when the total phytoplankton increased.

4. Myxophyta was the predominant phylum. The predominance of Myxophyta was due to the presence of *Anacystis* in excedingly high numbers. The Chrysophyta were next greatest in numbers and then the Chlorophyta with the Pyrrophyta occurring sporadically and in relatively small numbers.

5. The relative per cent of Myxophyta was inversely proportional to the relative per cent of Chrysophyta.

6. Nineteen genera of Chlorophyta appeared; *Ankistrodesmus, Scenedesmus,* and *Westella* occurred consistently in the collections. The greatest numbers of organisms and genera within the Chlorophyta occurred in the months of July through October.

7. Twenty-five genera of Chrysophyta occurred throughout the year. The diatoms, *Asterionella, Diatoma, Fragilaria, Melosira, Navicula, Nitzschia, Stephanodiscus* and *Cyclotella, Synedra,* and *Tabellaria,* were in almost all the collections. There was a tendency for the total numbers to be lower during the summer months.

8. Fifteen genera of Myxophyta appeared; *Anacystis* was the only genus present in every collection.

9. Pyrrophyta did not appear often in the collections and were represented by only 2 genera, *Ceratium* and *Peridinium.*

10. The temperature range apparently cannot be directly correlated with the productivity of any individual phylum and its effects must be considered in relation to the many other environmental factors which influence phytoplankton production.

11. Turbidity apparently affected the phytoplankton yield. In general, higher turbidities preceded a high phytoplankton pulse and during the pulse, the turbidity was relatively low. The turbidity was higher when the percentage of Chrysophyta per collection increased and con-

versely, the turbidity was lower when the percentage of Myxophyta and Chlorophyta per collection increased.

12. There appeared to be a tendency for higher saturation values of oxygen when the turbidities were low; however, the data did not show a consistent relationship.

13. During a 48-hour period of unusually calm water, collections were made every 6 hours. Definite population peaks were established, and the 2 lows were 24 hours apart. These incomplete data suggest that certain chemical factors, such as the bicarbonate supply, may have a decided effect upon phytoplankton productivity. Further work should be done by continuous collections at short intervals to evaluate the effects of these factors.

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THE FISH POPULATION OF A SPRING-FED SWAMP IN THE MISSISSIPPI BOTTOMS OF SOUTHERN ILLINOIS[1]

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INTRODUCTION

Pine Hills Swamp is located in the Mississippi River Bottoms a short distance north of Wolf Lake, Illinois (Fig. 1). It is situated at the base of a limestone bluff which was formed by cutting action of the Mississippi River. The Mississippi River now occupies a channel 5 miles to the west (Fig. 1). The limestone bluff, which is 150 to 350 feet high, shades a large area of the swamp at its base. At least 4 springs emerge from this bluff but only the northernmost spring considered in this paper provides a source of water for the swamp.

Primary emphasis was placed upon the fish population; however, a collection of other animals as well as aquatic plants was taken with the purpose of providing a more comprehensive view of this rather unique community. This work does not constitute a complete faunistic or floristic survey. The Pine Hills area is of interest to zoologists and botanists alike due to the fact that it represents a natural, undisturbed swamp area which probably contains much of its original flora and fauna.

METHODS

The fish population was sampled by means of hand dipnets, a 0.25-inch bar measure knot seine, and an electrical fishing device. The electrical fishing device consisted of a 230-volt alternating-current portable generator equipped with hand

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[1] This was a cooperative study between the Cooperative Fisheries Laboratory of Southern Illinois University and the Division of Fisheries, Illinois Department of Conservation. Mr. Sam Parr cooperated on behalf of the department.

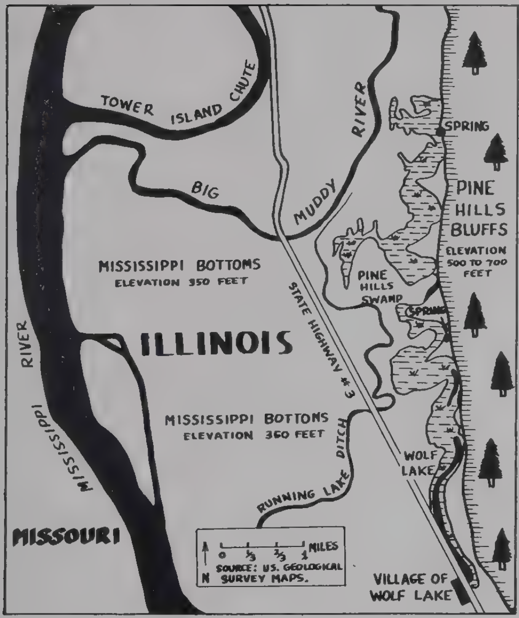

FIG. 1. The Pine Hills Swamp and its adjacent waters.

electrodes. In sampling the fishes, distinct samples were taken from each recognized plant community. Some reptiles and amphibians were also obtained by these collecting devices. The stomach contents of the fishes were examined. All animal collections were placed in the permanent collection of the Southern Illinois University Zoology Department. The plant specimens were deposited in the Southern Illinois University Herbarium.

AQUATIC FLORA

Twenty-five species of aquatic plants were collected from the swamp. The following plants were very abundant: mosquito fern (*Azolla mexicana* Presl.), and duckweeds (*Lemna minor* L., *Spirodela polyrhiza* (L.) Schleid, *Wolffia columbiana* Karst, *Wolffiella floridana* (Smith) Thompson). Green algae (*Spirogyra* sp.), hornwort (*Ceratophyllum demersum* L.), water-willow (*Dianthera americana* L.), and bur-reed (*Sparganium eurycarpum* Engeln) were abundant. Plants classified as common were as follows: yellow pond lily (*Nuphar advena* Ait.), brook-weed (*Samolus parviflorus* Raf.), bur-marigold (*Bidens frondosa* L.), red ash (*Fraxinus pennsylvanica* Marsh), green ash (*Fraxinus lanceolata* Borkh.), buttonbush (*Cephalanthus occidentalis* L.), willow (*Salix* sp.), lizard-tail (*Saururus cernus L.*), and cut grass (*Leersia oryzoides* (L.) Sw.), Manna grass (*Glyceria septentrionalis* Hitch.), ditch stonecrop (*Penthorum sedoides* L.), smartweed (*Polygonum* sp.), and watercress (*Nasturtium officinale* R. Br.) were locally distributed. Rare plants included wapato (*Sagittaria* sp.), frogbit (*Limnobium spongia* (Bosc.)), and swamp milkweed (*Asclepias incarnata* L.).

The above plants were associated in 5 recognizable communities. These communities and their characteristic vegetation are as follows:

1. Open-water community almost devoid of aquatic vegetation and interspersed by fallen trees. Composed 20% of sampling area. Water temperature ranged from 80 to 85° F.
2. Mosquito fern, duckweed, hornwort community. Composed 40% of sampling area. Water temperature ranged from 78 to 82° F.
3. Green alga, yellow pond lily, duckweed community. Composed 30% of sampling area. Spring water with temperature ranging from 61 to 65° F.
4. Green alga community in northernmost spring. Composed 5% of sampling area. Water temperatures ranging from 56 to 58° F.
5. Watercress community in stream leading from southernmost spring. Spring itself without vegetation. Composed 5% of sampling area. Water temperatures ranging from 56 to 58° F.

It was from these plant communities that the fish population samples were taken. The interrelationships of the various species of fishes and aquatic plants will be discussed under the headings of the various fishes.

FAUNA IN ADDITION TO FISHES

Pine Hills Swamp contains a variety of animals in addition to fishes. All of the animals hereafter mentioned were observed, collected, or known positively to be present.

The bullfrog (*Rana catesbeiana* Shaw), green frog (*Rana clamitans* Latreille), cricket frog (*Acris gryllus* Le Conte), long-tailed salamander (*Eurycea longicauda* Green), dwarf siren (*Siren intermedia* Le Conte), water snakes (*Natrix* spp.), common snapping turtle (*Chelydra serpentina* Linnaeus), and red-eared turtle (*Pseudemys scripta* Schoepff) are particularly abundant. The green tree frog (*Hyla cinerea* Schneider), the spotted newt (*Diemictylus viridescens* Rafinesque), and the cottonmouth moccasin (*Ancistrodon piscivorus* Lacépède) are present in limited numbers as compared to the above-mentioned species.[2]

The beaver (*Castor canadensis* Kuhl) was known to be present early in the study as a result of numerous fresh tree cuttings as well as the occurrence of active beaver huts and dams within the swamp. Trappers reported taking the raccoon (*Procyon lotor* Linnaeus), and the mink (*Mustela vison* Schreber).

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[2] Nomenclature of amphibians and reptiles is according to Schmidt (1953).

The great blue heron (*Ardea herodias* Linnaeus), and American egret (*Casmerodius albus* (Gmelin)) have established a heronry in the swamp area. The wood duck (*Aix sponsa* (Linnaeus)) was observed from winter until summer. Its presence during the summer indicates that it probably utilizes the area for nesting.

The Fish Population

Twenty-three species of fishes (Table I) were taken during the survey which extended from November of 1953 until June of 1954. The pirate-perch, mudminnow, starhead topminnow, spring cave-fish, pigmy sunfish, and small sunfish were found to be the most abundant. The mud pickerel, round sunfish, bluegill, warmouth, largemouth bass, creek chubsucker, carp, yellow bullhead, mosquito fish, and swamp darter were taken in limited numbers. Single specimens of the green sunfish, orangespotted sunfish, pumpkinseed, black crappie, golden shiner, brown bullhead, and bowfin were collected. Following is a discussion of the individual fishes taken in the Pine Hills Swamp. Special emphasis is given to those species that are more unusual.

Table I. *Species list of fishes collected in the Pine Hills Swamp*

Common Name—Scientific Name	Percent of Total Sample
Pirate-perch—*Aphredoderus sayanus* (LeSueur)	35.7
Mudminnow—*Umbra limi* (Kirtland)	17.2
Starhead Topminnow—*Fundulus dispar* (Agassiz)	14.2
Spring Cave-fish—*Chologaster papilliferus* Forbes	7.8
Pigmy Sunfish—*Elassoma zonatum* Jordan	7.1
Small Sunfish—*Lepomis symmetricus* (Forbes)	5.0
Mud Pickerel—*Esox vermiculatus* LeSueur	2.1
Round Sunfish—*Centrarchus macropterus* Lacépède	1.8
Creek Chubsucker—*Erimyzon oblongus* (Girard)	1.4
Carp—*Cyprinus carpio* Linnaeus	1.4
Largemouth Bass—*Micropterus salmoides* (Lacépède)	1.4
Mosquito Fish—*Gambusia affinis* (Baird and Girard)	1.1
Bluegill—*Lepomis macrochirus* Rafinesque	1.0
Warmouth—*Chaenobryttus coronarius* (Bartram)	1.0
Swamp Darter—*Etheostoma gracile* (Girard)	1.0
Yellow Bullhead—*Ameiurus natalis* (LeSueur)	0.4
Green Sunfish—*Lepomis cyanellus* Rafinesque	0.1
Orangespotted Sunfish—*Lepomis humilis* (Girard)	0.1
Pumpkinseed—*Lepomis gibbosus* (Linnaeus)	0.1
Black Crappie—*Pomoxis nigro-maculatus* (LeSueur)	0.1
Golden Shiner—*Notemigonus crysoleucas* (Rafinesque)	0.1
Brown Bullhead—*Ameiurus nebulosus* (LeSueur)	0.1
Bowfin—*Amia calva* Linnaeus	0.1

PIRATE-PERCH

Aphredoderus sayanus (LeSueur)

Hubbs and Lagler (1949) give the range of the pirate-perch as extending from southeastern Minnesota, southern Wisconsin, southern Michigan and the southern tributaries of Lake Ontario southward, west of the Appalachian Mountains and foothills, to the Gulf Coast as far as Texas. The pirate-perch is a lowland form found chiefly in creeks, muddy sloughs, and swamps of southern United States. This species prefers quiet waters with a muddy bottom.

In the present study the pirate-perch was found to be the most abundant species in the Pine Hills Swamp (Table I). It was collected in the green alga-yellow pond lily-duckweed community of the swamp as well as in the green alga community of the northernmost spring. During a collecting trip on May 14, 1954 at the northernmost spring, one of the hand electrodes of the electrical fishing device was pushed into a hole in the bluff from which the spring water emerges. After a period of one minute the electrode was removed and 42 pirate-perch, 25 mudminnows, 1 spring cave-fish, 2 pigmy sunfish, 1 small sunfish, 2 swamp darters, 3 yellow bullheads, 1 brown bullhead, and 1 mud pickerel came flowing out of the spring. Similar collections were also made at later dates. These results indicate that the species mentioned are able to go into or leave the spring at will.

Several of the 42 pirate-perch contained eggs. The total number of eggs in one female of 2.25 inches (57 mm.) total length numbered 769. It was impossible to determine whether or not the pirate-perch were spawning within the spring.

Stomach contents of 25 pirate-perch were examined. The major food items were chironomids, amphipods, and various aquatic insects. The specimens ranged from 1.3 to 3.0 inches (37 to 77 mm.) total length.

MUDMINNOW

Umbra limi (Kirtland)

The mudminnow ranges from Minnesota through the Great Lakes drainage and south to Kansas and Tennessee (Eddy and Surber 1947). In the current study it was found to be very abundant in the green alga-yellow pond lily-duckweed plant community of the spring-fed swamp area. A striking association was evident between the mudminnow and aquatic vegetation. It was found in greatest abundance on the bottom of the swamp within the large masses of green algae. Several specimens were taken in the northernmost spring, and two were collected in the southernmost spring.

The major food items in stomachs of 31 specimens ranging from 2.0 to 3.5 inches (51 to 89 mm.) total length included aquatic beetles, filamentous algae, amphipods, aquatic snails, and various insects. In addition one spring cave-fish was taken from each of two stomachs removed from mudminnows in the southernmost spring.

STARHEAD TOPMINNOW

Fundulus dispar (Agassiz)

Eddy and Surber (1947) list this species as occurring from Iowa to southern Michigan and southward to Arkansas and Tennessee. It is generally characteristic of quiet waters of lakes and swamps.

In the present study this species was taken in the open-water community and the green alga-yellow pond lily-duckweed community. The starhead topminnow seems to prefer open water to aquatic vegetation.

Stomach analysis of 14 specimens ranging from 1.25 to 2.25 inches (36 to 57 mm.) total length indicated that the major food items consist of snails, water fleas, chironomids, various diptera, and filamentous algae. The starhead topminnow apparently serves as a source of food for various predaceous fishes since remains of 3 starheads were found in the stomachs of a largemouth bass and a warmouth.

A ditch containing about one foot of water was located near the northern limit of the Pine Hills Swamp and was found to contain the starhead topminnow and the mosquito fish. Forbes and Richardson (1920) found that the mosquito fish is more likely to occur with either of the species of topminnows found in southern Illinois (*Fundulus notatus* and *F. dispar*) than are the two species of topminnows with each other. The mosquito fish and blackstripe topminnow occur together in Horseshoe Lake, Illinois (Gunning 1953) and in the Big Muddy River (Lewis 1954). All three of the above-mentioned species occur in Wolf Lake, Illinois.

SPRING CAVE-FISH

Chologaster papilliferus Forbes

The range of the various cave-fishes includes southern Illinois, southern Indiana, Kentucky, Missouri, and various southern states (Forbes and Richardson 1920). The spring cave-fish (Fig. 2) is an inhabitant of subterranean streams, caves, springs, and swamps.

In the present study specimens were taken from both of the springs sampled in Pine Hills (Fig. 1) as well as from the green alga-yellow pond lily-duckweed community of the swamp. In the swamp the cave-fish occurred with all of the fish listed in Table I except the golden shiner, yellow bullhead, and brown bullhead. In the northernmost spring it was present with the mud pickerel, small sunfish, yellow bullhead, brown bullhead, mudminnow, starhead topminnow, pirate-perch, swamp darter, and pigmy sunfish. The mudminnow was the only species occurring with the cave-fish in the southernmost spring. On several occasions it was observed that the spring cave-fish disappeared from the southernmost spring and its connected stream and reappeared at a later date. It appeared that the fish were periodically moving up into the spring and then moving out again. Subsequent field trips at night verified the belief that the cave-fish is nocturnal in habit. The cave-fish occupy subterranean habitat during the day and move out into the connected springs at night.

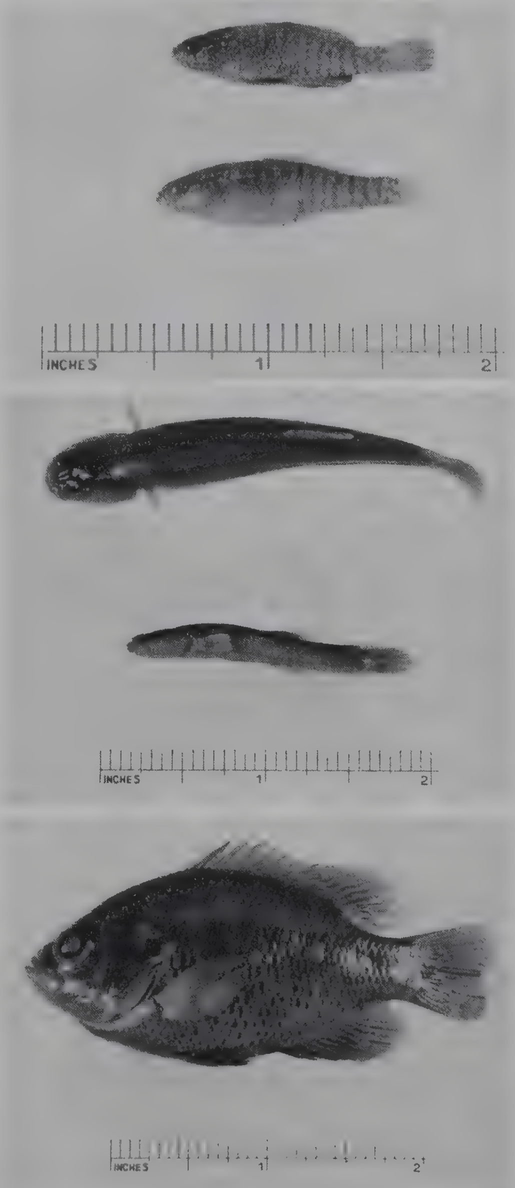

FIG. 2. Top, pigmy sunfish, *Elassoma zonatum* Jordan; middle, spring cave-fish, *Chologaster papilliferus* Forbes; bottom, small sunfish, *Lepomis symmetricus* Forbes.

The carnivorous feeding habits of the spring cave-fish have been noted by Forbes and Richardson (1920), Layne and Thompson (1952), and Weise (1953). Weise (1953) opened a few stomachs of specimens taken from the southernmost spring and found remains of the amphipod (*Gammarus troglophilus* Hubricht and Mackin). The stomach contents of 27 specimens examined in the present study were found to contain the same species of amphipod, insect remnants, insect larvae, and detritus. These specimens ranged between 1.0 to 2.9 inches (25 to 73 mm.) total length.

PIGMY SUNFISH

Elassoma zonatum Jordan

The occurrence of the pigmy sunfish in southern Illinois was noted by Jordan and Evermann (1896). The pigmy sunfish is characteristic of weedy bayous and backwater areas ranging south from southern Illinois to Alabama and west to Texas (Knapp 1953). In Illinois this smallest of the spiny-rayed fishes has been taken only from the waters in the Wabash Valley, Running Lake, and a bluff spring in Union County (Forbes and Richardson 1920).

In the present study the pigmy sunfish was taken from two plant communities in the Pine Hills Swamp and the northernmost spring. The pigmy sunfish was the only species of fish taken from the mosquito fern-duckweed-hornwort plant community. All of the fishes mentioned in Table I were present with the pigmy sunfish in the green alga-yellow pond lily-duckweed plant community except the golden shiner, yellow bullhead, and brown bullhead. Several specimens were taken from the northernmost spring which contained abundant green algae. Other fish in the spring were the mud pickerel, small sunfish, yellow bullhead, brown bullhead, mudminnow, starhead topminnow, pirate-perch, spring cave-fish, and swamp darter. Thus in one place the pigmy sunfish was well protected by a continuous mat of vegetation with no other fishes present and in the other it was present in a lighter vegetation cover along with several other species.

The condition in the green alga-yellow pond lily-duckweed plant community corresponds to a similar situation on a study area in Louisiana, which demonstrated that the pigmy sunfish is usually found with the mudminnow, mosquito fish, and various species of topminnows (Barney and Anson 1920). The Louisiana study area contained many of the species of aquatic plants found in the Pine Hills Swamp. The latter authors state that the adaptation of the pigmy sunfish to an environment of dense vegetation, with the total exclusion of other fishes that could prey on it, very much enhances its possibility of survival (Barney and Anson 1920). This might well be the case in the Pine Hills Swamp since the stomach of one mud pickerel contained a pair of pigmy sunfish and one warmouth stomach contained another.

Food analysis was made for 12 pigmy sunfish ranging from 1.0 to 1.5 inches (26 to 38 mm.) total length. The major food items were water fleas, rotifers, amphipods, chronomids, and small diptera.

SMALL SUNFISH

Lepomis symmetricus (Forbes)

In Illinois the small sunfish (Fig. 2) is found chiefly in the southern portion of the state, especially the Wabash Valley (Richardson 1904). Southern Illinois represents the northern boundary of its area of distribution (Forbes and Richardson 1920). The Cooperative Fisheries Laboratory at Southern Illinois University has records of this species only from the Pine Hills Swamp. The range of the small sunfish extends from Illinois through the central Mississippi Valley to Louisiana, southeastern Oklahoma, Arkansas, and Texas (Knapp 1953).

In the present study the small sunfish was collected chiefly in the green alga-yellow pond lily-duckweed plant community of the swamp. A single specimen was collected from the northernmost spring which is connected with the above-mentioned community by a small spring-fed stream.

The major food items occurring in the stomachs of 22 specimens examined were aquatic snails, green algae, amphipods, and miscellaneous insects and insect larvae. The specimens examined ranged from 1.5 to 3.3 inches (38 to 85 mm.) total length.

ROUND SUNFISH (FLIER)

Centrarchus macropterus Lacépède

The round sunfish ranges from Virginia south to Florida, west to Louisiana and east Texas, and north in the Mississippi Valley to southern Illinois (Knapp 1953). O'Donnell (1935) reports the round sunfish as being found in southern Illinois from Hamilton County southward. It has been taken only from creeks and sloughs tributary to the Little Wabash, Big Muddy, Cache, and a small creek near Brookport. This species was formerly abundant in Horseshoe Lake (Thompson and Bennett 1938), but has since disappeared (Gunning 1953). It is not known whether or not the round sunfish is still present in the other areas mentioned with the exception of the Pine Hills Swamp. Forbes and Richardson (1920) described the flier as a distinctly southern species, occurring in lowland streams and bayous of the lower Mississippi Valley.

Analysis of the 13 stomachs from specimens of 3.5 to 6.5 inches (89 to 165 mm.) total length showed that the major food items taken are insects, water fleas, amphipods, and filamentous algae.

The flier was collected in the present study only from the green alga-yellow pond lily-duckweed community in the spring-fed portion of the Pine Hills Swamp.

SWAMP DARTER

Etheostoma gracile (Girard)

The swamp darter is found in "the lowlands of the Mississippi basin extending north in river valleys to southern Illinois and Indiana, southward to extreme western Alabama and westward to central Oklahoma and the Nueces River in Texas" (Knapp 1953). In Illinois it is found in the southern part of the state especially in sluggish waters with a mud bottom. In the present study 7 specimens were taken from the spring-fed swamp area and the northernmost spring of the Pine Hills Swamp.

GAME FISHES

The largemouth bass, bluegill, warmouth, and mud pickerel populations were of a size and abundance that would permit utilization by sport fishermen, but the fish population of the Pine Hills Swamp is utilized very little due to its inaccessibility. The abundance of aquatic vegetation prevents fishing from the road which borders the swamp on the east side. Fishing from boats is prevented by logs, fallen trees, and shallow water.

The green sunfish, black crappie, yellow bullhead, and brown bullhead were not large enough or abundant enough to be of interest to sport fishermen.

MISCELLANEOUS FISHES

Miscellaneous fishes included the creek chubsucker, carp, mosquito fish, orangespotted sunfish, pumpkinseed, golden shiner, and bowfin. Several of these species were represented by a single specimen and the remainder were taken in such small numbers that a discussion of individual species was not warranted.

Discussion

The Pine Hills area is the approximate northern limit of distribution for at least five of the fishes found in the swamp. These species include the mosquito fish, round sunfish, small sunfish, pigmy sunfish, and spring cave-fish (Forbes and Richardson 1920; Knapp 1953). The remaining species of fishes (Table I) range into both the northern and southern United States. The swamp is also the approximate northern limit of distribution of the cottonmouth moccasin.

The steep limestone bluffs shading the Pine Hills Swamp afford a microclimate which is responsible for the distribution of the fish population as well as the development of unique plant communities. Mechanical protection provided by the aquatic plants plays an important role in the ecology of certain species of fishes as has already been mentioned. A definite contrast was obvious between the aquatic vegetation of the shaded area and the westernmost areas which are not shaded by the bluffs. The fish population was concentrated mainly within the shaded area.

The role of temperature in the microclimate was well illustrated in the spring-fed swamp area. The water temperature of this area ranged from 61 to 65° F. at which time the air temperature ranged from 85 to 100° F. All of the species of fishes listed in Table I except a single golden shiner specimen were represented in this area. In terms of numbers the spring-fed swamp area provided approximately 75% of the total sample. Contrasted with the spring-fed swamp area were the areas of open water that were sampled. The water temperature of these areas ranged from 80 to 85° F. at which time the air temperature was 80 to 100° F. Eleven starhead topminnows and one golden shiner were the only fishes collected in the latter areas. In terms of numbers the areas of open water provided only 3% of the total sample.

The scarcity of fishes in the open water might be attributed to selective mortality caused by a drought which has extended over a period of two years. The drought has served to lessen the water area of several portions of the swamp and other areas are dried up. The deepest portions of the swamp sampled in the present study did not exceed 5 feet in depth.

In conclusion it can be said that management in the Pine Hills Swamp should be directed along lines that would preserve the rare forms of plant and animal life. At present the area is relatively undisturbed. The authors feel that this area should be preserved since it represents one of the few natural habitats of its type in southern Illinois.

Acknowledgments

Thanks are due Mr. Roger Quentin Bell of the Southern Illinois University staff for identifica-

tion of the aquatic plants collected during the course of this study. The help of numerous students, especially Messrs. Darrell Louder, Charles Peters, and Ronald Newton, was appreciated.

SUMMARY

A study extending over eight months was made of the fish population, fauna in addition to fishes, and aquatic flora of a spring-fed swamp in the Mississippi River Bottoms of southern Illinois. The area was considered to be a good study area in that it represents a natural, undisturbed swamp which probably contains much of its original flora and fauna. Primary emphasis was placed on the fish population.

The swamp area presented a variety of plant communities from which fishes could be taken. These plant communities were characterized mainly by the following species of plants: mosquito fern, duckweeds (4 species), hornwort, green alga, and yellow pond lily. Individual plant communities and their contained fishes were listed along with the interrelationships between the aquatic vegetation and various species of fishes.

Southern Illinois is marginal range for the small sunfish, pigmy sunfish, spring cave-fish, mosquito fish, and round sunfish. The remaining species of fishes discussed range into both the northern and southern United States.

In conclusion it was stated that management in the Pine Hills Swamp should be directed along lines that would preserve the rarer species of plants and animals present as well as one of the last natural, undisturbed habitats of this type in southern Illinois.

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A PRAIRIE CONTINUUM IN WISCONSIN[1]

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The prairies of Wisconsin lie along the northeastern edge of the prairie peninsula (Transeau 1935). In pre-settlement times, they formed the matrix of the land cover in the extreme southwestern corner of the State, with scattered islands of deciduous forest. Toward the northeast, they gradually became the islands in a matrix of forest and disappeared altogether beyond a curving line (Fig. 1) connecting Osceola (44° 58′ N, 92° 40′ W) and Milwaukee (43° 2′ N, 87° 50′ W). Throughout this prairie-forest border region, the prairies occurred on a variety of land-form types, from alluvial or lacustrine flatlands through rolling uplands to steep bluffs and knolls. Altogether, they covered approximately 20% of the area, although this figure is greatly influenced by the difficulty of separating prairie from adjacent oak savanna and might be tripled if the savannas were included in the total. General accounts of the floristic composition or other features of the Wisconsin prairies have been given by Gates (1912), Shimek (1924) and Thomson (1940). Published, quantitative, phytosociologic investigations have been very few. Green (1950) studied the mesic prairies of Rock County by the quadrat method, while Curtis and Greene (1949) reported a study of prairies in the entire region based upon presence-lists. In the latter investigation, 65 prairies were classified into 4 groups upon the basis of land form or soil type (low, high, dry lime, and sand). The percentage presence was calculated for each species separately for each group. Only 84 species were found which occurred in at least one-half of the stands of any one group; only 19 species occurred in at least one-half of the entire series. Of the 84 constants, 72% occurred in some amount in all 4 prairie types. None was found to be restricted to one type only. It was possible, however, to pick out preferential species which could serve as indicators of each type on the basis of their occurrence with a presence in one type at least 10% greater than in any other type. There were 34 such preferential species for the low prairies, 11 for the high prairies, 14 for the lime prairies, and only 5 for the sand prairies.

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[1] The material in this paper was presented in a preliminary form based on data from the first 100 stations at the Minneapolis meetings of the Ecological Society of America in 1951. The investigation was supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

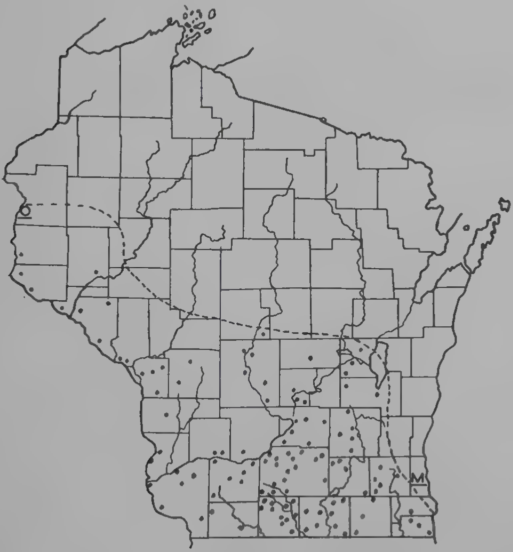

FIG. 1. Map of Wisconsin showing location of prairie stands studied. The dotted line connecting Osceola (*O*) and Milwaukee (*M*) represents the northeastern limit of the prairies.

These results clearly demonstrated that no discrete associations existed within the Wisconsin prairie community since the majority of the species were found in all types. However, the existence of high numbers of preferential species indicated modes of concentration which might be construed as the beginnings of community differentiation. The scarcity of preferential species in the stands with sandy soil showed that this factor alone was insufficient to greatly influence the floristic composition.

With this background, further work was initiated to determine whether the modes of concentration were really distinct and recognizable as incipient community types or whether the prairies formed a continuum of continuously varying species ranges as has been demonstrated in many communities (Ramensky 1938, Motyka *et al.* 1951, Curtis and McIntosh 1951, Whittaker 1951, Brown and Curtis 1952, Goodall 1954) and as was postulated as the underlying theory of community organization by Gleason (1926).

The present paper reports a study of 157 stands located in 34 counties, in an area of about 22,000 square miles. Presence lists were made in all 157 stands. In addition, frequency was determined in 57 stands by the use of 20 quadrats, each one meter square. I would like to express deep appreciation to Dr. Orlin Anderson for permission to use the results of many of his quadrat studies and to the following individuals who contributed greatly to the study in a number of ways: Dr. Grant Cottam, Dr. H. C. Greene, Dr. M. L. Partch, Dr. Roger Bray, Miss Phoebe Green, and Mr. Benjamin Wagner. The taxonomic nomenclature follows that of Gleason (1952).

METHODS

Criteria for selection of stands were the same as those used by Curtis and Greene (1949). As in the earlier study, none of the stands had ever been plowed and all were free from grazing although most of them were subject to at least an occasional burning or haymowing or both.

A marginal-punch card was prepared for each stand, showing which ones of the 84 constant species (arranged in alphabetical order around the border of the card) were present in the stand. As a means of classifying the stands, it was decided to pick groups of species which commonly occurred together and then to determine the relative distribution of these groups in all of the stands. This indicator-group approach was used by Kittredge (1938) in his study of Wisconsin aspen stands and has since been used for Wisconsin forest herbs (Gilbert and Curtis 1953). A first approximation in the selection of these indicators was made by choosing 3 groups of 10 preferential species with the highest average presence values in each of the 3 major prairie types as shown in the earlier study (Curtis and Greene 1949). For this purpose, the sand prairies were combined with the other types on the basis of their topographic position. Thus, the wet sand areas were combined with the other low prairies, the very dry sand areas with the dry prairies, etc. In this paper, the 3 major types are called wet, mesic and dry, rather than low, high and dry.

In addition to these 3 groups which had an obvious peak of occurrence in some one prairie type, there were many species which had high values in 2 consecutive types. Accordingly, 2 more groups of 10 species were chosen—those with high presence percentages in the wet and mesic prairies but low or missing from the dry prairies, and those low in wet prairies but high in mesic and dry sites. The resulting 50 indicator species, in 5 groups of 10 each, did not include many of the most ubiquitous prairie plants, such as *Amorpha canescens* or *Andropogon gerardi,* since these had high values in all 3 types.

It was a simple matter to determine the number of species in each group at each station by examination of the punch-cards. For example, a given prairie might have one of the wet prairie indicators, 5 of the wet-mesic group, 8 of the mesic group, 7 of the mesic-dry group and none of the dry group. This distribution was summarized by an index number, arrived at by making a weighted average of the group frequencies. The number of wet species was multiplied by 1, the number of wet-mesic by 2, the mesic by 3 and so on. The weighted numbers were summed and divided by the total number of indicator species present. In the above example, the calculation is as follows:

$$\frac{(1 \times 1) + (5 \times 2) + (8 \times 3) + (7 \times 4) + (0 \times 5)}{1 + 5 + 8 + 7 + 5} = \frac{63}{26} = 2.423 \times 100 = 242.3$$

The resulting presence index has a range of from 100 to 500. If a given prairie had indicators in the dry group only it would have an index of 100 while if the only indicators present were in the wet group, it would have an index of 500. An index of 300 could be obtained if the only indicators present were in the mesic group. However, any symmetrical distribution of numbers will also gave an index of 300. Thus, a series like 0-2-10-2-0 will give 300, as will a series like 5-5-5-5-5 or even 7-3-0-3-7. In actual practice, none of the 157 stands studied had a bimodal distribution. The indicators in all stands formed essentially normal curves or portions of such curves.

RESULTS

When this index was calculated for the first 100 stands, the punch-cards were arranged in the numerical order indicated by the index. As can be seen in Figure 2, such an arrangement resulted in a concentration of the occurrences of each species within a limited group of stands. Such a result might be expected for those species which were used in the construction of the index, but it applied equally to those species not used as indicators. The varied behavior of some of these non-indicator species is illustrated in Figure 3, which was prepared by calculating presence percentages for the stands in successive segments of 40 index numbers (100-139, 140-179, etc.). In this and all other graphs in this paper, the actual average points are plotted directly, with no arithmetic smoothing or other manipulations.

Similar curves were prepared for the 300 species most frequently encountered in the first 100 stands. Examination of the curves showed that some of the indicator species first chosen were less suitable than certain other species, in that they were irregular, covered too broad a range, or had a peak other than that initially estimated. Accordingly, such species (a total of 7 out of the original 50) were replaced by others which had a clear-cut optimum within the range of the appropriate group. This new list of indicators is shown in Table I. New indices were calculated for the first 100 stands and for the 57 stands studied later. All further results in this paper are based on these revised indicators and index numbers for the 157 stands.

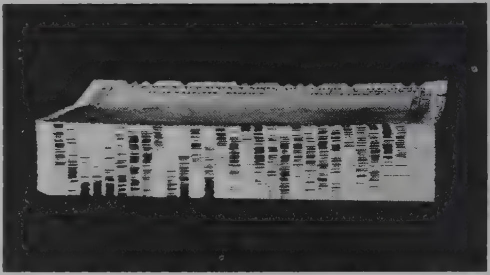

FIG. 2. Photograph of stack of marginal punch-cards which have been arranged in the numerical order indicated by the presence index. Notice the concentration of occurrences of many species in limited groups of adjacent stands.

TABLE I. *Average % presence of Wisconsin prairie plants by 50-unit size classes of presence index. All species are included which have values of 40% or more in any one size class. The indicator species in each group are marked with an asterisk*

Species	Midpoints of size classes						
	150	200	250	300	350	400	450
WET PRAIRIES							
Anemone canadensis	37	50	32	8	4	—	—
Aster novae-angliae	68	81	59	19	4	—	—
Aster paniculatus	53	44	18	4	7	—	—
Calamagrostis canadensis	95	81	54	12	—	—	—
Cirsium muticum	53	6	4	—	—	—	—
Equisetum arvense	63	50	41	27	4	—	—
Eupatorium maculatum	47	6	4	—	—	—	—
Eupatorium perfoliatum	33	6	4	—	—	—	—
Gentiana andrewsii	37	50	36	15	—	—	—
*Hypoxis hirsuta**	58	44	27	23	7	9	—
Lathyrus palustris	53	62	18	12	4	—	—
Lilium superbum	59	69	23	12	—	2	—
Muhlenbergia racemosa	42	12	23	15	11	2	—
*Oxypolis rigidior**	68	69	27	8	4	—	—
*Pycnanthemum virginianum**	74	88	73	12	11	9	—
Salix humilis	63	56	50	35	14	23	7
Saxifraga pensylvanica	47	38	14	4	—	—	—
*Solidago gigantea**	74	50	41	4	7	5	7
*Spartina pectinata**	95	81	54	27	4	—	—
Spiraea alba	58	50	36	4	—	—	—
Stachys palustris	27	44	23	—	—	—	—
*Thalictrum dasycarpum**	90	87	77	19	4	—	—
Thelypteris palustris	58	6	4	—	—	—	—
*Veronicastrum virginicum**	74	75	68	12	14	2	—
Viola cucullata	63	50	14	4	7	—	—
*Zizia aurea**	74	81	41	38	11	2	—
WET-MESIC PRAIRIES							
Allium canadense	16	19	32	8	7	—	—
Apocynum cannabinum	37	31	23	46	25	7	—
Asclepias syriaca	63	94	68	88	79	35	27
*Cicuta maculata**	16	56	36	—	—	—	—
Comandra richardsiana	37	81	59	65	54	53	60
Corylus americana	21	50	50	31	29	12	—
*Desmodium canadense**	42	69	54	58	32	5	—
*Dodecatheon meadia**	42	56	73	58	39	28	13
Elymus canadensis	5	69	50	50	54	30	13
Equisetum kansanum	16	38	54	27	25	12	—
*Fragaria virginiana**	79	94	64	62	29	2	—
*Galium boreale**	74	75	73	46	11	14	—
Geranium maculatum	26	69	36	35	11	—	7
*Helianthus grosseserratus**	58	88	64	46	25	5	—
*Heuchera richardsonii**	37	50	54	46	36	33	7
*Lathyrus venosus**	53	62	18	12	4	—	—
Liatris pycnostachya	26	44	46	12	7	—	—
Lobelia spicata	32	31	50	27	32	35	20
Monarda fistulosa	53	94	64	92	61	67	73
*Phlox pilosa**	58	62	54	65	50	7	7
Prenanthes racemosa	—	38	50	27	18	—	—
*Rudbeckia hirta**	63	75	73	38	54	33	20
Silphium terebinthinaceum	21	56	36	38	11	2	—
Smilacina stellata	21	50	32	27	18	23	13
Solidago graminifolia	16	38	41	23	7	2	—
Tradescantia ohiensis	47	69	73	69	43	54	13
MESIC PRAIRIE							
Achillea millefolium	32	50	68	69	39	23	13
Andropogon gerardi	68	100	96	100	96	100	93
Apocynum androsaemifolium	—	19	14	50	50	28	7
Aster azureus	16	56	73	54	68	72	40
Aster ericoides	5	38	46	92	82	79	73
*Aster laevis**	5	62	68	100	75	28	47
Baptisia leucophaea	10	19	41	54	32	5	—
*Ceanothus americanus**	5	19	50	81	43	26	13
*Cirsium discolor**	26	69	64	77	61	23	—
Convolvulus sepium	21	12	32	65	43	19	20
MESIC PRAIRIE (cont.)							
*Desmodium illinoense**	5	19	32	77	32	26	20
*Eryngium yuccifolium**	10	19	54	62	54	12	—
Gentiana puberula	5	6	18	46	39	7	—
*Helianthus laetiflorus**	10	25	68	92	71	63	60
Heliopsis helianthoides	21	31	18	46	18	12	7
Lactuca canadensis	5	44	41	46	61	26	27
Lespedeza capitata	—	25	77	69	46	40	13
*Liatris aspera**	—	6	54	92	86	84	27
*Panicum leibergii**	16	44	68	73	64	54	27
Physalis virginiana	—	19	4	50	57	37	40
*Ratibida pinnata**	37	81	96	96	79	70	40
Silphium integrifolium	21	38	50	54	39	23	7
Silphium laciniatum	10	25	41	65	43	26	7
*Solidago missouriensis**	—	50	27	62	46	37	7
Solidago speciosa	—	12	23	62	68	19	13
Sorghastrum nutans	10	31	59	65	64	58	27
MESIC-DRY PRAIRIES							
*Anemone cylindrica**	—	19	27	58	79	67	67
Antennaria sp.	16	19	41	65	64	70	60
*Asclepias verticillata**	5	—	27	35	54	74	73
Coreopsis palmata	5	12	54	85	86	72	80
Hedeoma hispida	—	—	—	4	32	74	67
Helianthemum canadense	—	6	23	15	43	19	—
*Helianthus occidentalis**	—	6	27	46	50	35	33
Liatris cylindracea	—	—	4	4	29	68	63
*Linum sulcatum**	—	—	—	12	18	56	27
Lithospermum canescens	16	44	50	69	54	72	40
Oenothera biennis	5	31	36	27	61	63	53
*Panicum oligosanthes**	5	—	9	42	54	65	27
*Petalostemum candidum**	—	6	32	38	43	42	20
*Potentilla arguta**	10	6	41	65	75	79	47
Rhus glabra	—	50	41	46	61	65	33
Rosa blanda	37	81	86	96	79	91	93
*Scutellaria parvula**	—	—	9	8	18	63	47
Sisyrinchium campestre	16	19	36	46	36	56	47
Solidago rigida	32	62	82	81	82	79	73
*Sporobolus heterolepis**	—	50	64	73	71	88	80
*Stipa spartea**	—	6	50	73	82	93	47
Viola pedata	—	—	9	15	43	44	33
Viola pedatifida	5	—	18	54	39	49	33
DRY PRAIRIES							
*Andropogon scoparius**	—	38	59	69	82	95	100
*Anemone patens**	—	—	9	4	25	67	93
Ambrosia artemisiifolia	5	44	50	62	64	74	80
Amorpha canescens	5	25	64	85	93	95	100
Arabis lyrata	—	—	—	—	7	30	40
*Arenaria stricta**	—	—	—	4	14	53	93
*Artemisia caudata**	—	—	4	15	36	81	87
Aster oblongifolius	—	—	—	4	14	58	60
*Aster ptarmicoides**	—	—	—	4	25	47	60
*Aster sericeus**	—	—	—	27	61	87	93
*Bouteloua curtipendula**	—	—	4	4	57	87	100
Castilleja sessiliflora	—	—	—	—	7	41	42
Erigeron strigosus	42	25	57	27	54	63	87
Euphorbia corollata	26	62	73	81	93	93	93
Geum triflorum	—	12	9	8	21	42	60
Koeleria cristata	—	—	23	31	36	49	60
Kuhnia eupatorioides	—	6	9	15	32	77	87
Lithospermum incisum	—	—	—	12	14	67	87
*Panicum perlongum**	—	—	—	12	54	67	73
*Petalostemum purpureum**	—	12	59	62	71	91	100
Physalis longifolia	—	—	—	—	18	49	67
Psoralea esculenta	—	—	—	—	11	12	47
*Solidago nemoralis**	—	6	46	31	71	98	98
Verbena stricta	—	—	—	12	18	26	80

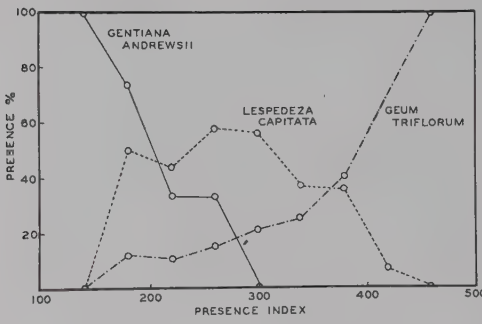

FIG. 3. Behavior of three non-indicator species when plotted against preliminary stand index. Wet prairies are at the left of the index and dry prairies at the right.

The behavior of a number of species is indicated in Figure 4 and in Table I. Examination of the curves for all species revealed that they formed a continuous series, from those with a peak at the left to those with a peak at the right. There were no distinct groups of species with similar curves and hence no groups of stands which could be differentiated from other groups on the basis of floristic composition. The 157 prairie stands thus formed a vegetational continuum, with a varying series of species of different ecologic amplitudes, each adapted to a slightly different set of optimum conditions and each behaving essentially independently of the others. The prairie herbs resemble both the herbs and the trees of the upland forests of Wisconsin (Curtis and McIntosh 1951, Brown and Curtis 1952, Gilbert and Curtis 1953) and the communities they form are indivisible into discrete entities, as was the case in the forests.

This assessment of a prairie continuum is based solely on presence information, which is perhaps the least precise measure available to the phytosociologist. Detailed statements of density and dominance, which are so valuable in the forest, are, as is well known, of limited utility in the prairie, due to the almost insurmountable difficulties of counting individuals or estimating basal areas. Quadrat frequency is perhaps the best method of gaining information on the quantitative relations of the prairie plants. The near equivalence in size of the plants permits use of a single, standardized quadrat area, thus greatly increasing the comparative value of the resulting frequency percentages.

Average frequency percentages were calculated for all important species in the 57 stands which were examined by the quadrat method. Some of the results are plotted in Figure 5, together with the presence percentages. As is usually the case in such comparisons (Gilbert and Curtis 1953) the two sets of figures are very similar, with frequency giving more clearcut results in the regions of high presence (as in *Andropogon gerardi*), while presence seems better when its values are low and frequencies thus too low to be indicative (as in *Panicum oligosanthes*). In another approach to the comparison, it was found that the sums of frequency for the indicator species in each group were highly correlated with the actual number of indicator species. The very close correlation strengthens the evidence that the stand order based on presence only would not have been significantly changed had it been possible to base it on frequency values instead.

Environmental correlations

The particular order of stands indicated by the presence index was originally based upon an external factor—namely topography and hence indirectly on water It is assumed that the same order could have been achieved had one of the species-correlation methods been used instead (Agrell 1945, Motyka 1950, Goodall 1954, de Vries 1954). In fact, it might have been obtained by a variety of methods or might have been approximated by a subjective judgment based solely on intimate field knowledge of the behavior of the species concerned The fact that practically all species involved produce smooth curves, conforming well to the basic premise of the ecologist concerning the nature of ecological adaptation, is taken as internal proof of the correctness of the arrangement. Presumably, the vegetational continuum should correlate with some environmental gradient along which the species have become sorted. Since light and temperature are relatively similar in all of these prairie types, the soil and the soil water seem good possibilities for such a gradient.

In most of the stands studied, 3 separate collections of soil were pooled and analyzed for available calcium, magnesium, potassium, phosphorus, nitrate, ammonia, pH, and water-retaining capacity.

An approach to the problem of water supply was investigated by the method used by Partch (1949). The stands were segregated into groups based on the water-retaining capacity of their soils (divided into 20% size classes) and the presence percentages calculated for each species in each group of stands. The behavior of selected species is shown in Figure 6. These results are very similar to those found in a detailed study of a single wet prairie made by Partch.

No distinct correlations of soil nutrients with

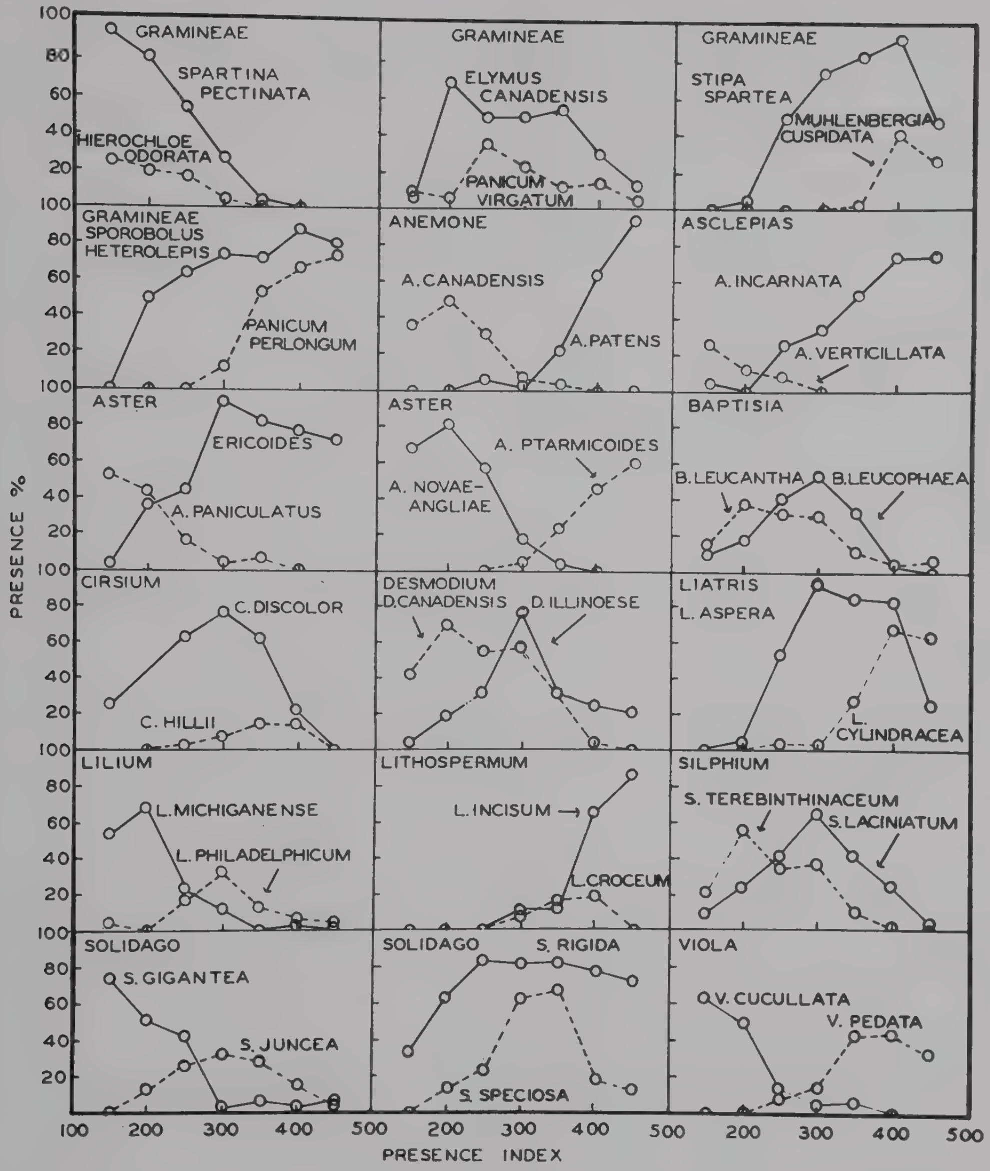

FIG. 4. Behavior of several grasses and forbs when plotted against final index. Notice the very divergent patterns shown by species in the same genus. Wet prairies are at the left and dry prairies at the right.

plant distribution could be found. The underlying data were highly variable and seemed to indicate the possibility of a slight trend for magnesium and phosphorus but no correlation with calcium, potassium, nitrate or ammonia. The overall averages for analyses from 51 stands in pounds of available nutrients per acre were: calcium 8160 lbs., magnesium 948, potassium 230, phosporus 108, nitrate 2.9, and ammonia 48.

DISCUSSION

The prairies of Wisconsin are a fairly distinct physiognomic vegetation type. They grade into the sedge meadows on very wet sites and into the deciduous forest on all sites through an intermediate savanna—the "oak opening." Within the prairie proper there is a continuously changing series of species, from those best adapted to sea-

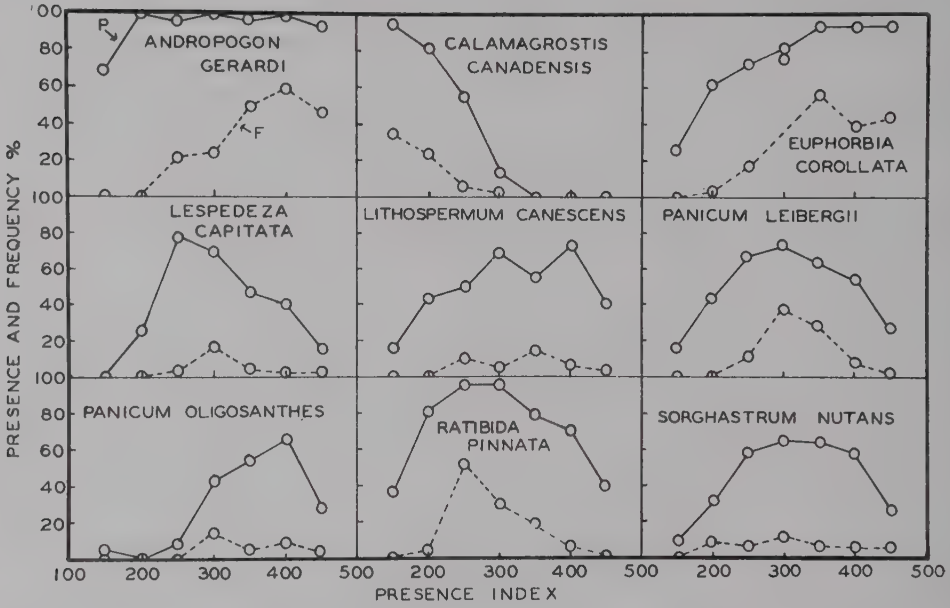

FIG. 5. Comparison of presence and frequency percentages for a series of species of varied behaviors.

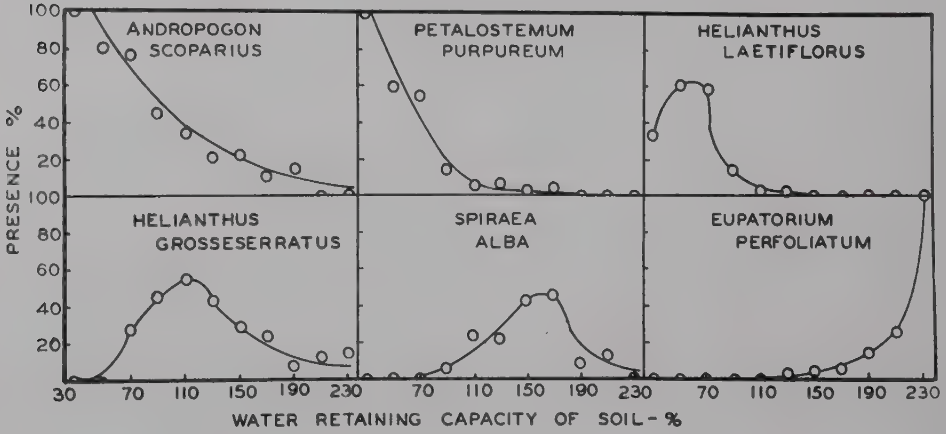

FIG. 6. Presence curves for selected species, based on stands grouped into 20% size classes of water retaining capacity.

sonal inundation and poor soil aeration in the wet prairies, through those best adapted to a deep mesic soil of high fertility and good drainage, to those adapted to very dry conditions as brought about by very thin soils over bedrock or other conditions of excessive soil drainage. Since these topographic types are not themselves discrete but rather grade into one another, the mixtures of plants are likewise not discrete. There appears to be no dynamic mechanism in the prairie which tends to purify a given stand for a particular group of species. The major dominant, *Andropogon gerardi,* occurs throughout all of the prairies and the other dominants, *Calamagrostis canadensis, Spartina pectinata, Sorghastrum nutans, Stipa spartea,* and *Andropogon scoparius,* each cover a large portion of the prairies. Any tendency toward species replacement due to differential shade tolerance, as is found in the deciduous forest, is here concealed by the continual internal disturbance in the prairie occasioned by burrowing mammals, colonial ants, or other movers of the soil. Thus, while there well may be a theoretical succession from pioneer to climax species on any microsite, no large areas are ever in the same stage of succession at the same time and no opportunity to differentiate developmental communities exists.

There is no evidence whatever that the wet prairies are capable of becoming mesic prairies through any reaction their members may have on the habitat, nor can the dry prairies so change their environment as to become mesic. The centripetal trend may be present, but the only motivating force which can bring about its accomplishment is the slow geological base-leveling which will reduce the hills and fill the valleys. Under such circumstances there is little to be gained by a discussion of either a single theoretical climax prairie with various subclimax types, or a group of edaphic climaxes. Rather, the prairies of Wisconsin are to be considered as part of a larger physiognomic formation with a unity of structure imparted by the dominant grasses.

The formation occurs on a wide variety of topographic sites, from the driest in the State to the very wet, but not the wettest. A few species occur in considerable importance over the entire moisture gradient (*Andropogon gerardi, Euphorbia corollata, Lithospermum canescens, Solidago rigida*), but most species are adapted to a lesser portion of the gradient and some reach high levels of importance only within a very narrow segment of the ecocline. Each species differs from every other in the exact shape of its amplitude-of-tolerance curve and no groups of species of reasonably similar behavior are present except for those at the ends of the gradient. These end groups, made up of species which reach highest importance (as measured by presence or frequency) in either the driest or wettest sites studied, are in reality artificial groups. They would disappear as groups if stands in the wetter sedge meadows had been included, or if stands from Iowa or Nebraska had been used to extend the dry end of the series.

One of the interesting results of this study is the clear separation frequently shown in the ecologic behavior of related species in the same genus (Figure 4). The larger genera, such as *Asclepias, Aster, Liatris,* and *Solidago* have species which peak in all sections of the continuum. No important genus has all of its species with optima in the same general region of the gradient. This ordination method of recording the behavior of species may be a step in the direction proposed by Dansereau (1952) when he urged that the full description of a given taxon must include a measure of its ecologic adaptations as well as its morphology and its genetics. Preparation of similar behavior diagrams for all communities of occurrence of a given species or for similar gradients in other portions of its geographical range would contribute as much to our understanding of the species as would the most comprehensive monographic treatment based on morphology alone.

SUMMARY

1. The prairies of Wisconsin were studied by means of presence lists made in 157 remnant stands on a variety of topographic sites in 34 counties covering an area of about 22,000 square miles. In addition, quadrat frequencies based on 20 quadrats each one meter square were determined in 57 of the stands. Soils were analyzed for volume-weight, moisture-holding capacity, pH and available nutrients.

2. Several groups of indicator species were chosen, based upon high percentage of occurrence in a topographic type. An index was calculated for each stand by determining the relative occurrence of each indicator group in each stand and making a weighted summation of the values.

3. When the stands were arranged in the order given by the index, all species, both indicators and non-indicators, were found to form smooth curves of occurrence, with a peak in some restricted portion of the stands. Some species had very broad amplitudes of occurrence while others were narrowly limited. No groups of species of similar behavior were found. The entire species complement formed a continuous series, from those growing best in the wettest sites to those growing best in the driest sites. As a result of this spread in species behavior, the stands themselves formed a continuous series, or vegetational continuum, with no discrete community entities present.

4. When the stands were grouped into classes based on water-retaining capacity, and the percentage presence calculated for each species for each class, the resulting curves showed the same relations as before. No significant correlation could be demonstrated between species composition and any soil nutrient, within the range studied.

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STUDIES ON TERRITORIALISM AND SEXUAL SELECTION IN DRAGONFLIES[1]

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In recent years territorialism has been studied extensively in vertebrates, but the invertebrates in general have received little attention. It is the writer's opinion that territorialism is related to sexual selection, and the insects, such as dragonflies, whose mating activities are highly localized and overt, are well suited for such studies.

There has been considerable controversy about the functions of territories and, consequently, about definitions. Noble (1939) has presented a general definition of territory as "any defended area" thereby leaving function to be described in relation to a particular case. Noble's definition will be used throughout the following discussion with an attempt at an analysis of function.

Darwin (1871) included dragonflies among insects illustrating his concept of sexual selection, and other naturalists have reported apparent displays of bright colors. Tillyard (1912) observed that males of *Libellago caligata* wave their long white inferior appendages toward females before copulation while the females replied to these signals by showing the white underside of the tip of the abdomen. Williamson (1906) says, "In *Rhinocypha* and *Calopteryx* the sexes are attracted to each other by movements and displays of color." Williamson was also of the opinion that the specific colors of male dragonflies are important in bringing about conspecific mating. He supported this view by pointing out the uniformly similar abdominal appendages of species with highly colored wings, in contrast to the specifically distinct appendages of colorless-winged species. He postulated that the influence of the male colors operated as an isolating mechanism among some genera, whereas the complex genitalia isolated the species in others.

Some indications that dragonflies show territorial behavior have been recorded. Williamson (1889) says that males of *Celithemis elisa* "make sudden dashes at passing diptera and smaller dragonflies, often returning to the same sedge time and time again. Each is the proprietor of a particular locality. When one encroaches on the hunting territory of another he is quickly hustled away by the rightful and irate owner." Byers (1930) indicates defence of territory on the part of males of *Tetragoneura semiaquia*. Lieftinck (1934) describes males of *Crocothemis servilia*, "struggling for the mastery of their domain in the pursuit of other dragonflies." Wiliamson (1923) states that males of the genus Erythemis protect their own females against attack during oviposition. Whitehouse (1941) observed a male of *Plathemis lydia* poise on the wing above an ovipositing female with which he had mated and drive away other males.

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[1] Contribution no. 534 from the Zoological Laboratories of Indiana University, Bloomington, Indiana.

Saint-Quentin (1934) made an attempt to study territorialism among dragonflies by means of marked individuals. He observed that dragonflies roam in restricted areas in which they tolerate no similar dragonfly. This behavior was interpreted as the eviction of intruders from the hunting ground, termed "ein Jagdrevier." Since none of the marked dragonflies was recovered, Saint-Quentin concluded that the Jagdrevier was of a transitory nature. He also noted that dead aeschnid males suspended by strings were attacked by other males.

Moore (1952a) repeated the work of Saint-Quentin using live male dragonflies suspended from strings and found that attacking males would sometimes couple with the suspended ones. Moore was successful in recovering some of his individually marked specimens, but failed to find any constancy in localization. He concluded that the inability of dragonflies to recognize sex results in inter-male clashes bringing about temporary dispersal throughout the breeding area to simulate territorial behavior.

Opinion has been divided in regard to whether there is inter-male competition among dragonflies. Williamson (1906) reports males of Libellula fighting for females. Walker (1912) in his studies of the genus Aeschna says there is no contest between males for females nor are the males apparently able to distinguish females of their own species from those of other species of the genus. Needham (1929) observed males of *Pachydiplax longipennis* meeting in combat. Hingston (1933) in interpreting animal adornment as an instrument of hostility includes the dragonflies and other insects in theoretical support.

The present investigation on the dragonflies *Plathemis lydia* (Drury) and *Perithemis tenera* (Say) was conducted in an attempt to obtain evidence on the following questions: (1) Do the bright colors of the males induce differential male mating success and, if so, is this because of the effect of these colors on females? (2) What sexual isolating mechanisms are operative? (3) Are territories maintained and, if so, what are the functions of these territories?

I wish to thank Dr. F. N. Young for his active interest and advice and for his help in the preparation of the manuscript, Dr. W. H. Thorpe for having reviewed the manuscript, Dr. T. W. Torrey for his care in seeing that photographic and other materials were provided, Dr. B. Saila for giving statistical advice, and Mr. R. H. Marlin for allowing free access to the pasture pond where part of the studies were conducted.

SPECIES AND LOCALITIES

A series of observations was made on the behavior of dragonflies at ponds near Bloomington, Indiana. The two species selected for concentrated study differed greatly in behavior and were abundant in the area. A brief description of the species is as follows: *Plathemis lydia*, herein simply designated as Plathemis, was selected to represent a sexually dimorphic dragonfly in which male "display" to the female was not observed. The mature male abdomen is white dorsally, and the wings are clear with a dark median band. The female abdomen is dark, and the wings bear a median and terminal dark spot. *Perithemis tenera*, herein designated as Perithemis, was selected as a sexually dimorphic dragonfly in which males appear to "display" to the females. The male wings are amber in color except for a small dark spot near the triangle in some individuals. The female wings are clear with two dark spots on each, the degree of spotting being highly variable.

One of the situations at which observations were made was a small solution pond about 10 km. north of Bloomington, Indiana. It is circular, about 128 m. in circumference at the water's edge, and during the period of observation was about 0.6 m. deep except during heavy rains when it became as much as 0.9 m. deep. The sink in which the pond is located was first plugged in 1946 following ploughing of the field and has contained standing water since that time (*fide* Mr. R. H. Marlin, property owner). The pond contained little floating or emergent vegetation except around the edges where Potamogeton, sedges, grasses, and algae were found.

Observations were also made at an excavated pond about 1.6 km. north of the solution pond. This pond is rectangular measuring about 161 m. by 27 m. by 0.9 m. deep. The northeast and south banks are forested and partly shaded. The west bank has been cleared, and numerous stumps project into the water. The long axis of the pond lies north and south.

Other observations were made at an elongated reservoir, Wiley Lake, about 1.6 km. north of the excavated pond. Since the lake is surrounded by steep heavily wooded hills, most of the shore is partially shaded. In these shaded areas there is little aquatic vegetation. Along the sunny parts of the shore, the western and southeastern parts, patches of Potamogeton partly covered with algae are found.

METHODS

In catching dragonflies for marking, a net held open by means of wires was used to prevent injury to the specimens. When tenerals began to emerge, in May, as many as feasible were caught and marked with spots of paint in front of the thorax. Different color combinations were used on each day. When adults arrived at the pond after maturation, all the males and some of the females were individually marked with paint shot at them with a syringe or, as was usually possible, they were captured and marks of paint were placed on the wings and sometimes on the dorsal surface of the abdomen. Enamel paint was used exclusively.

The wing markings consisted of a dot about 4 mm. in diameter placed on the center of the median patch of the wing, a vertical line through the patch, a streak filling the costal cell of the patch, or a combination of the streak and vertical line. Any or all of the wings were marked in various combinations following a constant order. Yellow and aluminum were used exclusively for wing marking. Specimens thus marked could be identified even in flight.

Egg samples were obtained by dipping the abdomen of captive females into vials of pond water. The vials were shaken to scatter the eggs and were then laid on their sides until the eggs stuck to the glass. Eggs thus separated hatched readily at room temperature if the water was changed daily. If the water was not changed, or if the eggs were clustered, many failed to hatch.

In 1952 at the solution pond, Plathemis was observed from May 1 to June 17, and Perithemis from June 17 to July 31. In the Plathemis studies the pond was circled continuously each day when the species was active. The activities of Perithemis were observed from a vantage point overlooking all available oviposition sites. (Sites out of observation range were removed.) Further observations on Perithemis were made at Wiley Lake from August 1 to September 14, 1952 and at the excavated pond from June 6 to July 17, 1953.

A pond under study was visited daily from early morning until late evening when the last dragonfly had left (except during cool cloudy weather when dragonflies failed to arrive). Each time a specimen was observed its activities and location at the pond were recorded. Records of air temperature and cloudiness were made at regular intervals. At the end of the day, observations were tabulated. From time to time the results were analyzed statistically. In the following discussion "±" refers to standard error of the mean.

STUDIES ON PLATHEMIS

Observations on Behavior

Emergence of Adults. In 1952 the first teneral Plathemis was observed on May 1. Emergence continued through August. The naiads usually began creeping from the pond shortly after sunrise and continued until about 11:00 A.M. (CDT). They crawled into the grass usually 1-5 m. from the pond, but sometimes as much as 45 m. Solitary sandpipers captured large numbers of naiads on the shore, and kingbirds preyed upon tenerals flying toward the woods nearby.

Teneral Adults. The sex ratio of marked tenerals was 129:209 or 1 male: 1.62 females. This possibly does not indicate the true sex ratio, since males are more active than females and more readily escape capture. Of the marked tenerals, only 9 males and 6 females returned to the pond after maturation. Males returned a minimum of 8 and a maximum of 14 days after marking, and females a minimum of 13 and a maximum of 24 days. Although this may indicate that males return earlier than females, it could be only a sampling error. It is interesting, however, that some males show signs of immaturity upon return to the pond. Borror (1934) in his studies of *Argia moesta* notes that when adults are about 14 days old they return to the river to mate, the males by this time being almost or entirely pruinose.

Teneral males closely resemble females in color, but upon returning to the pond after the maturation period, males differ strikingly from the fe- white, or white abdominal pruinosity. Among seven males which were still bluish-brown after returning, and for which complete color notes were obtained, the pruinosity changed to bluish-white during the first day at the pond, and to white after 2-6 additional days.

Male Behavior. Single males appearing at the pond cruise over about one quarter of the margin while flying close to sites at which females are later seen ovipositing. A lone male usually spends considerable time near one site which he repeatedly approaches very closely, sometimes stimulating oviposition by dipping the tip of the abdomen into the water after the manner of a female. The oviposition sites consisted of clumps of mud, matted vegetation, or sticks, logs and similar objects floating in water near shore. Sites with glistening surfaces seemed especially attractive to males, which would usually stay near them. Often the male would perch near the site.

When a female appears, the male flies quickly toward her with his abdomen lowered, thus apparently hiding the white upper surface. In some cases, especially when the temperature was below 20° C. and the male was sluggish, he would apparently hide behind objects while flying toward the female. As the female slows down near a site, or begins oviposition motions, the male seizes her with his feet and immediately fastens his abdominal claspers to her head.

Copulation occurs in the air usually close to the site where the male had been localized. In copulation, the female allows her wings to rest and wraps her feet around the male's abdomen. Timing of 200 undisturbed copulations showed the duration to be about 3 seconds and remarkably constant. After copulation the male usually places the female on the site. The female may oviposit where she has been placed, or may flit around the pond to another site. In any event, the male follows her and hovers above her when she begins to oviposit, as if guarding her.

In no case was a male observed to guard a single female without first having copulated with her or with another female in the same area shortly before. If the abdomen of the male was stiffened by a heavy layer of paint, thus preventing him from bending his abdomen to fasten the abdominal claspers to the head of the female, he would repeatedly seize ovipositing females with his feet sometimes as often as 25 times in 20 min. In no case, however, was such a male observed guarding an ovipositing female.

After oviposition, when the female flies from the pond, the male follows her closely until she rests in the field. The male then returns to the area where oviposition had occurred. No male was observed attempting to seize a female which was resting in the field or on an oviposition site.

If a male is guarding an ovipositing female and another female flies to the site, the male may catch the ariving female and, after copulation, place her near the other and guard both. If the arriving female dives to the site and begins to oviposit while the male is guarding, the male will guard both ovipositing females without having copulated with the second. If the second female takes flight, however, the male may catch her and, after copulation, replace her with the first and continue guarding. When one of the females stops ovipositing and flies, the male follows her then returns and guards the other.

Usually many males are active at the pond. When two males encounter one another, one male dashes at the other and pursues him. The pursuing male raises the white upper surface of the abdomen toward the new arrival, while the latter flies away with abdomen lowered. This appears to be a joint display of the conspicuous upper surface of the abdomen. After the second male has been "chased" 8-16 m. from the site over which the first had been active, the first usually turns and flies back with abdomen lowered while the second now pursues with abdomen raised. This pursuit display, alternating in direction, continues until the new arrival restricts his movements to the vicinity of another site.

If the newly arrived male stays for some time around the site of the first, and especially if he simulates oviposition thereon, a dual flight may follow. This flight is often preceded by the two males facing each other immediately over the site with abdomens raised (Fig. 1). They then fly quickly upward, usually to a height of about 3 m., level off, and fly side by side, or one a little behind the other, back and forth across the pond and adjacent fields. The speed of such flights, timed with a stop watch, was found to approximate 7.5-10.7 m./sec. in still air. It is obvious

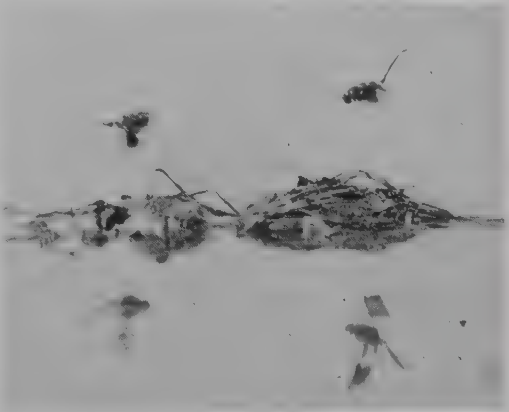

FIG. 1. Two Plathemis males mutually displaying the white upper surfaces of the abdomen near an oviposition site.

that the flight is not a speed test, for when one of the males is slowed by means of varnish placed on the wings, the other keeps pace with him. The flight may be interrupted after as little as one second or may continue for as long as 123 seconds, the mean of 37 samples being 40.5 seconds. One of the males seems to initiate the flight by suddenly flying up near the other. In a few cases males seemed consistently to refuse what appeared to be challenges to dual flight on the part of newly arrived males. After the flight, both males return to the original area and, after a little more pursuit display, one retires from the area.

As more males arrive, the interactions increase in complexity. The edge of the pond soon becomes populated with males each of which flies back and forth more or less parallel to the shore over a distance of about 9 m., about 4 m. on either side of one or more oviposition sites. It was found that the 128 m. circumference of the pond was thus normally divided into 12 sectors with lateral dimensions of about 11 m. The males in these sectors appeared to defend them against the intrusion of other males. When two males meet near the boundaries of their sectors they may first execute pursuit display, but gradually begin to avoid each other and sometimes perch in their sectors. Since there are usually more males present than sectors, pursuit displays and dual flights take place almost constantly in favorable weather. This activity appears to be partly responsible for continuous displacement of males throughout the day.

There was considerable disparity in number of matings (copulations and accessory events) which occurred in the sectors (Table I). There appeared to be more male interaction in those sectors in which most mating occurred. It also appeared that females mated and oviposited more readily at certain oviposition sites in much-used sectors. The eggs are laid in a glistening mass on the sides of projecting objects. Such glistening surfaces appear to attract both males and females and prodigious numbers of eggs may be laid at one spot.

TABLE I. *Distribution of 6,243 matings of Plathemis in the twelve sectors at the pond. Sectors are identified by means of compass directions*

Sector..........	NNE	N	NNW	SSW	S	SSE
Matings........	3%	6%	10%	12%	12%	12%
Sector..........	ESE	E	ENE	WNW	W	WSW
Matings........	2%	13%	8%	7%	9%	6%

Each sector had distinct characteristics; thus, the SSW sector contained numerous clumps of matted vegetation in addition to abundant emergent vegetation. The S and SSE sectors contained little emergent vegetation and few clumps of matted vegetation. The WNW sector was the only one with cattails. The ESE, E, and ENE sectors contained mostly grasses, and the NNE and N sectors mostly sedges. All the sectors changed aspect during the season so that only a general description can be given.

The excess of males over available sectors leads to many deviations from the pattern of lone male activity. In many cases a very active guarding male fails to ward off numerous others which are dashing at the ovipositing female. A male catching a female under these conditions flies with her in tandem over the pond in a jerky flight deflecting pursuing males from the course and finally returns to the site where copulation occurs. When other males disturb the copulating pair, copulation may last up to 15 sec. instead of the usual 3 sec. At such times the male appears to drive off rivals while he holds the female in a rather safe copulation position, then he releases the female when in a suitable position to dash at rivals (Fig. 2).

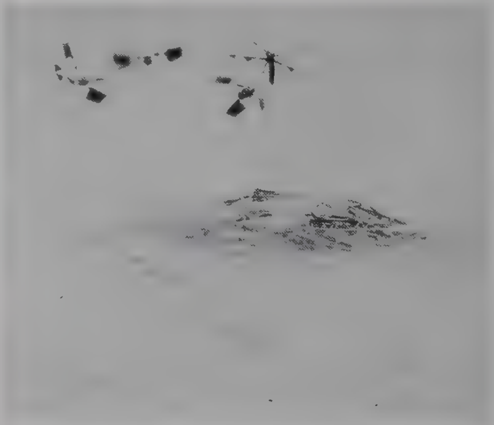

FIG. 2. Plathemis male releasing a female at an oviposition site while interacting with other males.

In many cases the female is chased by other males or is seized while ovipositing. When the female is seized, the guarding male becomes intensely active, flying toward other males and warding them from the site. In the meantime the male which seized the female copulates with her, then after replacing her on the site, guards her. The original male then dashes at the female and often catches her, then after copulation replaces

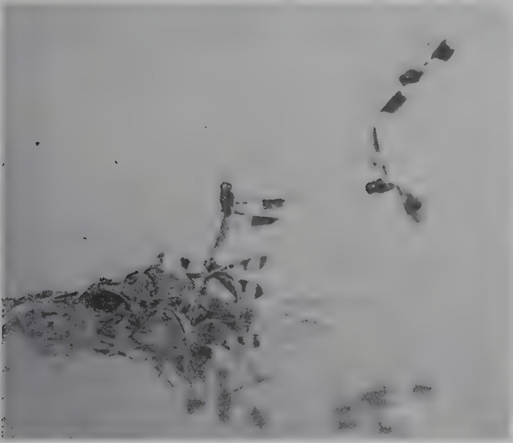

Fig. 3. Plathemis male seizing an ovipositing female as other males rush in.

her on the site. Many males may be involved in this process at one site leading to a melee in which they dash at one another swiftly (Fig. 3). Although males seldom contact one another, occasional collisions occur, after which one may drop into the water. During one of these melees the female may perch motionless on the site whereupon males will not seize her. (It appears they cannot see her, for if a female stops suddenly on the site, a pursuing male may assume the coupling position on the female's shadow or wing spot.) In these cases the female, being unable to oviposit, may fly from the pond followed by many males, some of which have come from adjacent areas. Kingbirds may fly into these flocks and catch males or, more frequently, the slower-flying females.

When two males simultaneously begin seizure of a female she may be injured and drop into the water. Wolf spiders (Dolomedes) often catch such females. With loss of the female, the males continue pursuit display and dual flights until many leave.

When a female does not oviposit on the site at which the male places her, but flies to another site, the guarding male follows her closely but does not seize her unless she dashes away suddenly. In such cases the female is frequently chased by other males. When a guarded female arrives at the site where another guarded female is ovipositing, the two guarding males do not interact strongly, but the visiting male soon retires while the other guards both females.

Males could be classed according to whether they arrived at the pond daily in the forenoon or afternoon: 13% of the marked males arrived mostly in the forenoon, and 60% mostly in the afternoon. The other 27% were too irregular to classify. The sequence of arrival of some of the males from day to day was quite constant.

Immature males fly in a slower, more fluttering manner than older males and show greater tendency to perch. They were frequently observed chasing males of *Anax junius* as if mistaking them for females of their own species. This reaction soon disappears as if they had learned to ignore Anax males. When a Plathemis female arrives, the immature males dash toward her immediately. They often made abortive copulations while flying for an extended period with the female in tandem. Although the female was usually soon released, one pair rested in the grass about five minutes before separating.

Immature males are easily driven away by the older males, but return from time to time. Such males, without a sector, if successful in capturing a female and copulating, may release her where no oviposition site is available. In such cases the female flies away without ovipositing. Immature males, if successful in holding a sector and mating, are less active in guarding than older males.

Some males showed definite localization to specific sectors. Many returned immediately to sectors previously occupied after having been absent from the pond for as long as five days during cool cloudy weather, indicating that memory may be involved. Many males showed affinity to specific oviposition sites in their sectors.

When many males are present, immatures show little localization the first days at the pond. After localization is established, perhaps on the fifth day, it may be maintained for perhaps ten additional days before declining. This analysis is based on complete records of only 20 males. This small sample makes quantitative statements tentative. However, the general statements are supported by shorter observations of many more males. Of the 20 immatures, 8 showed almost absolute localization during the 10-day middle period, but averaging all 20 males for this period showed that they were observed in their respective sectors a mean of only 42.5% of the times observed.

The mean daily number of matings of the 20 immatures increased during the period of increasing localization, while those of mature males marked on the same dates did not show the increasing localization nor an increase in mating number. The mating scores of all males showed decline with decline in localization. These data apply only when there is intermale competition and seem to indicate increasingly aggressive behavior with maturation.

The maximum period any of the immatures was present at the pond was 36 days, with a mean of 14.25 ± 2.00 days. Examination of the testes of 60 blue-brown, 88 blue-white, and 140 white males showed progressive degrees of encystment and spermiogenesis.

Males marked when blue-brown were less likely to repeat at the pond than were those marked when white on the date of their first arrival. Thus, of 137 males marked when blue-brown only 70, or 51% repeated one or more days, but of 127 marked when white 105, or 83% repeated. Though this may indicate heavier predation of immatures, it may also indicate a tendency for them to wander more than matures. In Perithemis there was a marked tendency for both sexes arriving early in the season to fly high and away from the pond after only brief examination. Perhaps a tendency to wander on the part of immature dragonflies is important in dispersal even in the absence of reaction between individuals.

There was an increase in the number of males present at the pond as well as in the number of matings from May 1 to June 17 when observations were ended. The maximum number of marked males recorded on any one day was 148: the daily mean for June was 104, and for May, 15. (Thirteen cool cloudy days in May were not counted.) During the first two weeks of July, Plathemis males were removed because studies of Perithemis were being started. Plathemis males dash at male and, especially, female Perithemis.) All males were taken from one sector by netting, or shooting with a BB air rifle while they were perched. In the two-week period 388 males were removed. The maximum removed on any one day was 130. When many mature males were removed, immatures gradually took their places.

Most matings occurred between 2-3 P.M. (generally the warmest part of the days). Males most in evidence at this time of day had higher mean daily mating scores than did those most in evidence during the first and last hours of observation. Perhaps males customarily arriving at the pond in the afternoon fresh from the woods, where they may have been feeding or resting, would be in a condition to compete with greater vigor and mate oftener than those arriving when few females are present, but when energy must still be expended in maintaining a site.

Female Behavior. On each day the first individual to arrive at the pond was a male, followed by a female after a mean of 41.0 ± 1.5 min. with a minimum of 1 min. in one case and a maximum of 110 in another. An arriving female flits about oviposition sites around the margins of the pond and may make oviposition motions on several sites. At such times a male may seize her. If, after copulation, the female is prevented from ovipositing, as when chased by other males or when no sites are available, she darts from males chasing her, except when near an oviposition site where she may slow down and be captured.

During oviposition the abdomen is struck into the water, thus washing off eggs against the site where they stick in a slimy mass. Undisturbed oviposition lasts 1-2 min. in which time 100-175 dips are made. Ovipositing females are easily approached. An ovipositing female seized by a male and carried to a site nearby, or chased from a site by the observer, usually returns to the original site to complete oviposition.

Of 60 females marked after capture while ovipositing, 44 returned to the pond and oviposited after one or more days. The maximum number of times a female was observed to return was 7 (within 22 days). Returning females showed a tendency to oviposit in the sector of previous oviposition.

Females are attracted to other flying females or to other dragonflies such as *Anax junius* or *Libellula basalis*. They are also attracted to ovipositing females of their own species, the tendency leading to communal oviposition. The attraction of an ovipositing female seems greater than that of an oviposition site alone. It is interesting that Perithemis females follow not only one another but also males which fly slowly to the site during events leading to courtship. Plathemis females were never observed to follow mature males of their own species, but in two instances females followed, for short distances, immature males with which they had copulated. Since immature males fly in a less jerky fashion than mature ones, flight pattern may be partly responsible for inducing following by the female. No dragonflies which females were observed to follow move in the jerky manner of mature Plathemis males. Females would also follow other Plathemis females with abdomens painted white so as to resemble males, but which do not fly like males.

EXPERIMENTAL REMOVAL OF MALES FROM THE POND

To determine whether older males prevented newly arrived immatures from localizing, all males but a few immature ones were continuously removed, May 20-29, 1953. With 140 males removed, the few remaining immatures showed almost absolute localization to a sector from the time they first arrived. The sector taken did not always seem suitable to females. Thus, May 21, most matings were taking place in a certain sector at submerged logs. At 1 P.M. all males were removed. At 2 P.M. an immature male arrived (for the first time) at a sector where no oviposition sites were present. In spite of the fact that the submerged log sector was vacant and remained so, the immature male did not visit that sector, but stayed in the sector first encountered. Females arriving flitted around the submerged logs but, no male being present, they flew around the pond until they encountered the male in the sector where no sites were available. The male there copulated with all six females arriving that afternoon. These females left without ovipositing after flitting around sedges in the sector.

With most of the males removed, the remaining males mated far more frequently than usual. It had been found that the mean daily mating scores, computed by dividing the total number of matings of a male by the number of days that male was present at the pond, did not exceed four under ordinary conditions. The males remaining after most of the others had been removed, however, averaged 80 matings per day. A male would apparently mate with as many females as would enter his area. After having mated 20 or more times, males became less active, perched much, and were easily driven from the pond by newly arrived males. In egg samples obtained from ten females which had mated in succession with one immature male, hatching occurred in all but the seventh and ninth. Of 33 samples from females which had copulated with the few remaining males, hatching occurred in 23. Of 50 samples taken June 1, after removal of males had been discontinued, hatching occurred in 46.

With all males removed, females still came to the oviposition sites and some oviposited alone. Females arriving for the first time (perhaps virgins) sometimes performed oviposition motions at sites, but soon flitted around the pond and gradually became very active in chasing other dragonflies for short distances. If two such females were present at the pond they were not only attracted to one another, but performed dual flights much as do males, after which one would leave the pond. Only a few females were therefore present at the pond at one time when males were absent. No difference in this behavior was noted among females when some of their abdomens were painted white so as to resemble males. No female was observed to remain at the pond more than ten minutes when no males were present. In many cases they rested in the field, returning occasionally, then flying to the woods.

Experimental Darkening of the Male Abdomen

Since it appeared that the white upper surface of the abdomen was employed by males as a threat, experiments were performed to test this hypothesis as well as to determine whether the white color induced differential male mating success. In addition to the regular identification marks the upper surface of the abdomen of one of each three males marked during the study was painted black, another white, and a third left unpainted, 164 of each type being marked. Enamel paint was used and was confined to the individual abdominal segments, since it had been found earlier that painting the intersegmental areas prevents the males from bending their abdomens to clasp the females.

The males were observed closely to determine whether the darkening induced any differences in behavior, especially in regard to mating success. Reactions of females to marked males were also studied. The study was continued for fifteen days.

In compiling data, repeating males having blackened abdomens were compared with an equal number having whitened abdomens marked on the same dates and in the same sectors. Males having whitened abdomens were similarly compared with unpainted ones. In finding the mean daily mating score of a male, the total number of observed matings of that male was divided by the number of days he arrived at the pond. The mean daily mating score of a group was the average of these means. It was thought that perhaps 90% of all matings that occurred were observed.

Results. The mean mating score of the blackened males was significantly below that of the whitened ones (Table II). The lower mating success of the blackened males appeared to result from their lowered ability to ward off opponents. It was frequently observed that an intruding male flying toward a site would depart when the guarding male displayed his white abdomen at him even though the guarding male made no dash at the intruder. The blackened males displayed their abdomens at rivals, but the display seemed less effective. Those blackened males that were most successful in warding off opponents appeared to do so by greatly increased activity in dashing at intruders and performing dual flights with them. In one case while a white male was guarding a female, a male with his abdomen stiffened with an excess of black paint pounced on the female repeatedly, but the guarding male did not react appreciably to the blackened one.

TABLE II. *Mean daily matings of Plathemis males with painted abdomens*

Treatment	Number of Males	Mean Mating Score	Sum of Squares
Whitened........	68	0.886	10.23
Blackened.......	68	0.731	9.62

"t" = 2.34.

When there was an "aggregation" of white males, the blackened ones were often absent. Blackened males had a tendency to "aggregate" in the NNE sector where relatively few matings occurred. When it became cloudy and many white males departed, blackened ones often appeared in their places. Only 27% of the white males returned to the pond during the last hour of observation during the study, but 33% of the blackened ones did so. Perhaps blackened males lingered longer at the pond as a result of being inhibited by whitened males when most mating was occurring in mid afternoon.

Decreased mating success of the blackened males did not appear due to failure in attracting females: rather, males seize females often from behind and lower the abdomen to such an extent that it sometimes drags in the water. The white upper surface is thus not displayed to females as it is to other males.

Information concerning the influence on the male of white color was obtained by painting the upper abdominal surface white on 30 females. In a few cases males performed pursuit displays toward these females as they do toward other males. Usually, however, males seized whitened females as if they were ordinary. After copulation, a guarding male would fly toward the whitened ovipositing female and, when she flew, seize her and copulate again. This was repeated by the same male until the female flew away. A guarding male would also dash at spots of white paint on logs, dead males, or, especially, white feathers moved by the wind near the site.

Comparison of the mating scores of whitened and unpainted males showed no significant difference. The mean mating score of 60 whitened males was 0.925 as compared with 0.950 on the part of 60 unpainted males marked on the same dates and in the same sectors. The observed "t" value was 0.206.

STUDIES ON PERITHEMIS

Observations on Behavior

Male Behavior. On first arrival at the pond, males fly slowly along the margin and closely approach floating patches of Potamogeton, algae, roots, sticks, or logs. When thus engaged, the males make short dips at the site as does an ovipositing female, but the male does not bend down his abdomen as does a female. This activity will be referred to as examination of the site (Fig. 4). At this time the male is easily approached, but if an attempt is made to capture him he will fly away particularly readily. Having established himself at a site, the male hovers over the water within a radius of about 30 m. but returns occasionally to fly over the site. He may then perch near the site at a position commanding a view over the open water.

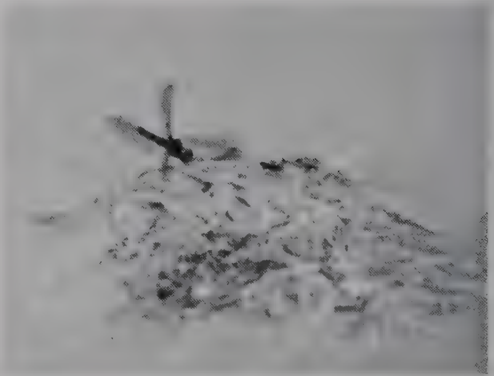

FIG. 4. Perithemis male performing examination behavior at an oviposition site.

When a female flies over the pond the male dashes toward her and follows her while swaying from side to side. He then turns and flies slowly to the site while the female follows, or if she does not follow flies after her again. Upon reaching the site, the male hovers intensely on it while fluttering his wings and sometimes bending up his abdomen. This activity will subsequently be referred to as courtship (Fig. 5). After the first courtship, or after several, the female's wings beat more slowly or stop while she perches on the site nearby. The male catches her as she flies slowly or perches, and fastens his abdominal claspers to her head. A male may apparently lose a perching female though she is only a few inches away. A male may assume a coupling position on the dark wing spots of a perching female as if mistaking them for a head.

In initiating copulation the male flies while supporting the female whose wings are at rest: he then perches, and copulation continues. Perhaps actual copulation does not begin until the female perches, for copulation time including the period

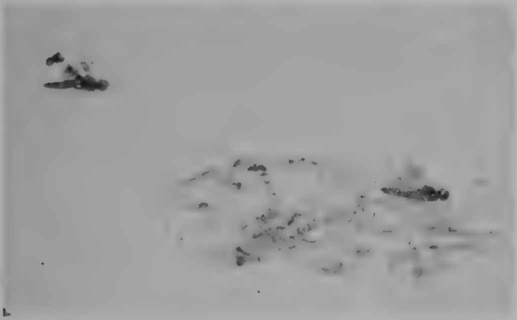

FIG. 5. Perithemis female following a male to the oviposition site.

when the pair was in flight in copulating position was highly variable, while if only the period of perching during copulation was considered, the time was often quite constant: such timing showed one male to copulate almost exactly 14 sec. with each of five females in succession.

On the whole, copulation time was variable; constancy prevailed only for short periods. One male copulated 17 sec. with each of four successive females from 11:00 to 11:40 A.M. June 29, 1953. Four other copulations for that male on the same day ranged from 15 to 20 sec. On July 1 he copulated 23 sec. with each of four successive females from 10:50 A.M. to 1:50 P.M., the only matings that day.

Copulation time seemed to depend on the male, for the same female would copulate long with a long-copulating male or briefly with a short-copulating male. The duration was often prolonged in shade or when the air temperature was below 25° C. Stop-watch timing of 623 undisturbed copulations of 25 males in sunlight at temperatures of 30-32° C. showed the mean duration to be 17.5 sec. If the copulating pair was disturbed by the observer, copulation sometimes lasted as long as 90 sec. Perhaps the male held the female until safe conditions prevailed.

After copulation the pair separates and the male flies slowly back to the site while the female closely follows. In some cases the female seemed to lose the male, whereupon he returned and led her to the site. Upon returning, the male hovers low over the site while the female slowly approaches. When the female begins to oviposit on the site, the male flies about her, dashing at any male intruders. If the ovipositing female begins to leave or is chased, the male follows her, whereupon she may follow him back to the site where he hovers until she resumes oviposition.

In many cases the female repeatedly avoids capture by a male at a site and finally fails to follow him, whereupon the male performs the activity described above as examination of the site.

It seems to require five minutes or more of examination before a male establishes himself at a site. If a female arrives while a male is still in the early stages of examination, the male may wander instead of leading her to a specific spot: the female quickly leaves in these cases.

If, while a pair is copulating, the oviposition site is removed, the returning male hovers near where the site had been, while the female follows. The female then flies to another site and oviposits alone, or the second male may court and catch her as usual.

If not ousted by other males, the male stays at one site throughout the day and returns to it on succeeding days with little or no re-examination. If the site is moved slowly to a new position, the male will follow and on subsequent days return to the new position. However, if a site is blown about the pond by the wind, it is soon vacated. Males would also vacate sites if the nearby water level lowered to less than about eight inches. Sites near steep banks in deep water were most used.

A male was rarely present at the pond alone for more than ten minutes. It was remarkable that regardless of the time the first male arrived, be it 8 A.M. or 3 P.M. he was succeeded by many others in about 15 minutes. When a second male arrives and encounters the first male, the latter dashes at him. If the second male had been at the pond previously, he would fly quickly to the site of the previous day and only occasionally encounter the first male. If the sites are at least 3 m. apart, the males gradually avoid encounters and perch near their sites. When many sites are available, the males come to be spaced about the pond at regular intervals of about 3-5 m. in areas including a site and sufficient water space to allow for flights over the water without extra-male molestation.

Males arriving at the pond for the first time may fly from site to site performing examination behavior. The localized males fly about them wildly and make roundabout flights over the pond. If the newcomer persists, wing fluttering may occur, the males hovering a few inches to a foot or more apart and making quick up and down movements over the site (Fig. 6). The duration of this activity may last a few minutes to an hour. Departure of one of the males is often preceded by the two facing each other in the air. Sometimes departure does not occur until after a pursuit flight, one male following the other at relatively great speed over the water in low roundabout

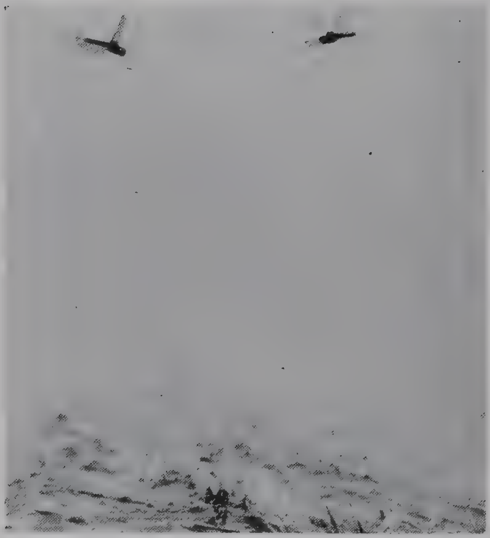

FIG. 6. Two Perithemis males fluttering their wings near each other.

flights. Such flights may last to 30 minutes. A departing male may leave the pond or fly to another site.

The initial spacing of the day requires little time, for the previous residents take their places quickly. As newcomers arrive, there is considerable wing fluttering at sites, the appearance being strongly reminiscent of flocks of "dancing" male Diptera. During such periods of violent activity many males leave the pond, and the organization becomes more tranquil. This tranquillity is again disturbed throughout the day as males return to the pond or as newcomers arrive. Usually there was complete displacement of localized males in the forenoon and another in the afternoon. The daily time of arrival of some males was remarkably constant and differed from male to male. Some males arrived daily in the forenoon and others in the afternoon.

Since the number of sites was limited, males sometimes took sites that were evidently unsuitable, for females consistently flew from courting males at these sites, then copulated at other sites. Males at these unsuitable sites frequently performed examination behavior and flew to other sites from time to time only to be driven away by male occupants of these other sites. Males repeatedly unsuccessful in obtaining sites flee readily when dashed at by other males, the flight being straight, like that of a female. This straight flight seems to induce male pursuit.

Instead of leading a female directly to a site, a male may deflect this course from another male's area as though aware that the occupant may interfere. Males from other areas often do pursue a female being led by another male, and a mass chase ensues. In these cases the female may fly until the number of males diminishes, whereupon she may turn and follow one of them. Extra males often make it impossible for a female to mate or oviposit, whereupon she may leave the pond, perch, or fly to another site.

Males examining sites were sometimes preyed upon. Wolf spiders (Dolomedes) were observed to catch six males, water bugs (*Belostoma lutarium*) four, fish two, and frogs (*Rana catesbeiana*) two. When a number of males are available, vacancies left after predation are quickly filled. If the male has been caught after the organization has become stable, however, the vacancy may not be filled for hours. Attraction of females to these sites by males is thus temporarily halted.

With bright sun and temperatures approaching 37° C. the males skew their wings causing a shadow to fall on the body, while they point their abdomens toward or away from the sun preventing the rays from striking the abdomen perpendicularly. The ordinary horizontal position is resumed when clouds obscure the sun.

Female Behavior. Each day, the first female arrived at the pond 10-30 min. after the first male. The organization was, therefore, relatively stable by the time the females began to arrive. During courtship at the site, the female may perch almost immediately, or fly and avoid capture by the male until she has been led back a number of times. If the female, after courtship, flies too rapidly to a perch and the male loses her, she may return to the site and, after further courtship, fly more slowly toward the perch where the male catches her. If an open net is placed over a courting male and moved slowly from the site, the female may follow the net in which the male hovers.

During copulation, the female wraps her feet around the male's abdomen. If, after copulation, the male flies back to the site too rapidly the female may apparently lose him, whereupon she may fly about and finally locate the site alone, but usually the male returns and leads her directly to the site. Both sexes showed a marked tendency to return to the exact spot where courtship had occurred and where the female had dipped her abdomen during courtship. In one case while a male was courting a female at one spot, the female repeatedly left and performed oviposition motions at a spot nearby. The pair copulated and oviposition occurred at the new spot. Thereafter, the male courted females only at the new spot.

If a female flies away after courtship the male attracts her again, whereupon she may follow or go to another site and stop for a second male or continue to yet another. During oviposition a female may be chased by an extra male whereupon she may return repeatedly to the spot to oviposit before being chased again. At such times the male which has copulated dashes at the extra male, then leads the female back to the spot. If extra-male interference makes oviposition impossible the female may go to another site where she is usually courted as a newcomer and may mate as usual, or may evade the male while ovipositing intermittently. In this case the male may pounce on the female and catch her; then copulation and oviposition occur in normal sequence. In this case the female may not copulate, but the pair flies in tandem about the site for an extended period while the male repeatedly bends his abdomen as in copulation. This behavior most nearly approximates what has been described as oviposition attended by the male. Needham (1929) says of this species, "The female is held by the male while ovipositing, but I have seen her oftener unattended, dropping her eggs on bits of floating dead pond skum by many successive dips at very nearly the same spot." Williamson (1899) says, "As in other related species (Celithemis and Sympetrum), the male retains his hold of the head of the female as she flies along near the surface of the water, occasionally striking the surface of the water with her abdomen to release the eggs." It seems unlikely, however, that Needham and Williamson were describing this rare behavior. In any case the writer has never seen the male hold the female during oviposition.

If an ovipositing female is netted and another female flies to the site and begins to oviposit, the guarding male does not usually court the newcomer but continues guarding. If the newcomer ceases ovipositing and begins to leave, or flies toward the male, the male may court her and copulation occur. Attraction of females to one another leads to communal oviposition. If a female arrives at a site where another female is ovipositing, the male may court or dash at either of the females. This may lead to re-copulation with the original female, copulation with the second, or chasing of one or both females from the site.

When all males are removed from the pond, the females fly to the oviposition sites, then either leave or oviposit alone. All of the egg samples (123) taken from females which had begun oviposition alone contained fertile eggs.

When ovipositing, the female dips her abdomen repeatedly toward the site and is easily approached when so engaged. If an attempt is made to capture her, she flies slightly from the site after each dip. In such cases she will continue oviposition more readily if the male is nearby, especially if the male has hovered on the site several times as he does after copulation. This behavior may have great survival value, for the male may here serve as an advertisement of conditions safe for the ovipositing female.

The egg masses "explode" in the water as observed by Montgomery (1937). This scattering may be important, for eggs in vials fail to hatch when clustered. Some females seem to lay their entire complement of eggs when their abdomens are dipped into vials of water: a few of the last eggs are sometimes small and presumably unripe. Counts of egg samples of 13 females which seemed to have laid unusually large numbers of eggs showed an average of 150 eggs with a maximum of 206.

Upon returning to the pond after the first oviposition, females showed a marked tendency to revisit the previous site. At Wiley Lake, where fourteen sites were being used, 150/394 repeats were at the previous site.

Females showed a peak of repeating after an interval of one day following the first oviposition (Table III). One female lived at least 34 days after the first oviposition.

Experimental Removal of Perithemis Males

From June 5, 1953 (when the first male of the season arrived) until July 19, only two males were permitted to remain at any one time in the vicinity of six sites on the east shore of the excavated pond. All other males were caught immediately

TABLE III. *Observed interval between first oviposition and repeated oviposition of 603 Perithemis females*

Days After First Oviposition	Number Repeating	Days After First Oviposition	Number Repeating
1	74	18	3
2	102	19	1
3	80	20	2
4	67	21	2
5	48	22	3
6	28	23	2
7	35	24	1
8	34	25	0
9	23	26	0
10	22	27	1
11	13	28	0
12	13	29	1
13	14	30	1
14	10	31	0
15	11	32	0
16	5	33	0
17	6	34	1

as they arrived. Egg samples were obtained from all females mating with these remaining males. This study gave further insight into the behavior of the species.

The remaining males showed almost absolute localization to particular sites throughout their duration at the pond and mated with the numerous females coming to these sites. After frequent copulation, the males often made abortive copulations and appeared weak. The time during which such males remained coupled to females was often prolonged. Under these conditions, the females were often observed to fly toward perching males and, in a few cases, pounced on them. After several days of abnormally high numbers of copulations, the males failed to return to the pond or, in two cases, left soon after returning. In one of these cases, after the male had mated 127 times in six successive days after first arriving at the pond, he returned the seventh day, mated one time, then left and did not return.

Egg samples from females with which the total of seven males had mated were checked for the approximate proportion of eggs hatching. Evidence of infertility of some or all of the eggs was found in the records of the three males for which most extensive records were obtained. No eggs hatched in a sample taken after the 43rd copulation of a male on the 8th successive day he had mated at the pond, and only about half of the eggs hatched in samples taken after the 45th and 46th matings of the same male on that day. The male returned next day, however, and copulated with four females whose eggs were fertile (perhaps they had been previously inseminated). The male returned on the 10th day, but left after about 15 min. without having mated and did not return.

The records of another male showed only about 10% hatching in a sample taken at the 15th (last) copulation on the first day at the pond, but a high percentage of the eggs hatched in samples taken after each of 85 subsequent matings of the male on seven additional days.

One male mated 8 consecutive days with a total of 101 females, but eggs hatched in high proportions in all samples. On the 9th day, however, the 2nd sample showed no hatching. On the 10th day the male returned, appeared inactive, and mated with only one female 25 min. after arriving: the eggs were fertile. After 45 min. he left and did not return.

Correlation of Weather and Behavior

In spite of wide fluctuations in air temperature, the mean number of daily matings (at least at temperatures 23-32° C.) was remarkably constant (Table IV). Activity was slowed at temperatures below 25° C. and appeared then to depend on warmth derived from sunshine. At temperatures above 30° C. activity was about as great in cloudy weather as it was in sunshine. A great increase in mating was often noted just before a storm, during hot humid cloudy conditions. At maximum daily temperatures of 23-28° C. only 12% of the matings were before noon, but at temperatures of 29-37° C. 32% were before noon. On days with a maximum temperature of 33° C. or higher, there was a lull in mating from 1-3 P.M. After unfavorable weather there was often an abnormally large number of matings.

TABLE IV. *Maximum air temperature and daily matings of Perithemis at Wiley Lake, 1952 and the excavated pond, 1953*

Maximum Air Temperature	Matings	Days	Matings/Day
23-24° C.	106	5	21
25-26° C.	244	9	27
27-28° C.	235	12	20
29-30° C.	570	25	23
31-32° C.	319	15	21
33-35° C.	347	11	32
36-37° C.	102	2	51

Tests of the Function of the Amber Color of the Wings

Observations of female behavior indicated attraction to males. It also appeared that females were influenced by courtship, since they would stop flying during such activity. If, while a female was being courted, the male was caught by a water bug and slowly pierced to death, the female would perch on the site while the male's wings were in motion, but when his wings finally stopped she no longer paused, but continued oviposition.

Following Darwin's views, one might suppose that the amber color influenced the female. Experiments were designed to test this hypotheses as well as the hypothesis that the color is employed in inter-male activity as had been found in Plathemis.

Live males and females were glued by their feet to sticks and placed near oviposition sites. Also, the wings of 200 males were blackened with shoe dye, while those of 200 controls were weighted with varnish thinned with turpentine to correspond roughly with the weighting effect of the shoe dye. The reactions of both sexes to the glued specimens and treated males were studied.

Interactions of Blackened-winged Males and Normal Ones: When a male with blackened wings flies to the pond, a localized male reacts to him as he does to a female: he flies toward the blackened male then turns and flies slowly to the oviposition site. The blackened male may follow, much as does a female. The normal male may court the blackened one at the site and, if the blackened male examines the site or flies slowly, the normal male may pounce on him, couple, and bend his abdomen into the precopulatory position. The blackened male is soon released, and after a few repetitions of this behavior the normal male fails to react to the blackened one. The blackened male may begin wing-fluttering near the normal male, but the latter fails to react and perches. The blackened male pounces repeatedly on the perching male, thus driving him away temporarily, but the localized male returns and perches again. After a time the blackened male may dash at and pursue the normal male over the water, but this flight usually is brief, and the blackened male leaves the area.

If a female arrives while the two males are in the area, she may follow either of the males to the site and be courted. Although it sometimes appeared that the female followed the normal male more readily than she did the blackened one, especially while she was being courted by a normal male or had copulated with him, this was not definitely determined. During courtship the female may stop and be captured by either male in the temporary absence of the other. It was not determined whether she would stop for a normal male more readily than for a blackened one.

When most males are removed and vacant sites are available, a blackened male leaving the area of a normal male may localize in a vacant area. A lone blackened male often seemed as successful in obtaining mates as the normal ones. Quantitative information on this point would be difficult to obtain, since mating success seems dependent on the nature and location of the site. Females may avoid capture by a blackened male at a site and copulate with a normal male at the same or another site, but the converse was found about as frequently.

When a blackened male enters the area of another blackened male, he is treated as a female. Upon reaching the oviposition site, the two blackened males may court each other simultaneously and may couple. They may later fail to react mutually and fly about the same area or perch as little as a foot apart. As many as six blackened males were observed "aggregating" in one area. Mating under these conditions was unsuccessful, for the females would be chased while following a male to the site.

Two or more blackened males may chase a normal male from an area by chasing him in turns, but a lone blackened male failed to do so except in a few cases after the normal male had mated a considerable number of times.

The males with wings weighted with varnish had a tendency to behave like blackened males, but the aberration (from normal) was less marked. These controls were sometimes treated as females by other males, so sex recognition may be partly based on flight pattern.

Reactions of Males and Females Toward Specimens Glued to Sticks. When male and dark female specimens (live or dead) are glued by their feet to sticks and placed near the site, the reactions of males toward female specimens differ from their reactions toward male specimens. Males bend their abdomens into the coupling position on the wing spots of female specimens or successfully couple with the head. On the other hand, they pounce repeatedly on the wings of male specimens without bending their abdomens. Coupling was most often observed among males which had just lost a female during courtship. Under these conditions a male would sometimes couple with a male specimen if the female specimen had been removed. With the female present, however, coupling was with that sex in all cases.

If a light female (with amber wings) was placed with a dark female and male specimen, the males reacted toward the light female sometimes as toward a male and sometimes as toward a female. Likewise, males, while wing-fluttering with other males, sometimes reacted to flying light females as if they were males: instead of courting the light female they would perform wing-fluttering with her and make roundabout flights over the pond. In such cases, males courted the light females after oviposition motions began.

Studies on Site Selection

Some males at the pond had much higher mating scores than did others. This disparity of mating seemed to depend, at least in part, on female choice. Some observations suggested that females were influenced by the attraction of the oviposition site in their apparent choice of males. Males localized at certain sites were consistently deserted by females courted there, while other males at the same time were mating repeatedly at other sites. One male held such a site for seven days while courting many females all of which avoided capture. This male did not differ appreciably in vigor or appearance from other males. Furthermore, a female would sometimes desert an ordinary male at one site where she was being courted, and mate with a blackened male at another site. At one site where most of the mating of the day was occurring, the male had battered wings (males may clash their wings with females during capture). With males removed, females continued oviposition mostly at sites where most mating had occurred when males were present.

To determine whether females differentially selected sites, a variety of sites were placed in the solution pond June 7, 1952. Two lines of small logs were tied end to end and floated parallel in the water about 5-9 m. from the shore. Patches of Potamogeton were fastened to the logs at about 5 m. intervals. All other sites were removed. At a position on the shore commanding a view of the sites, an observation tower was built.

Marked males were classed into three groups according to size of wing spot as correlated with density of body pigmentation. Males with a spot one-half mm. or more in any dimension were classed as dark, those with a spot less than one-half mm. as medium, and those with no spot, as light. Females were classed three ways according to degree of pigmentation of wings and body. Specimens which could not be classified were not considered.

Upon arriving at the pond for the first time, a male would examine a number of points along the logs and patches. Finally, apparently having selected a spot, he would perch nearby. The site might be a stick or log projecting from the water or a patch of Potamogeton. If a male was displaced from a stick or log and selected another site that day or on following days, he would usually select another stick or log, while other males, would as consistently select patches of Potamogeton. The females, returning to oviposit, behaved similarly. Of all repeaters, 91% of the males and 92% of the females could be classified according to whether they selected sticks or patches.

A comparison of the records at the end of July, 1952 suggested that dark individuals of both

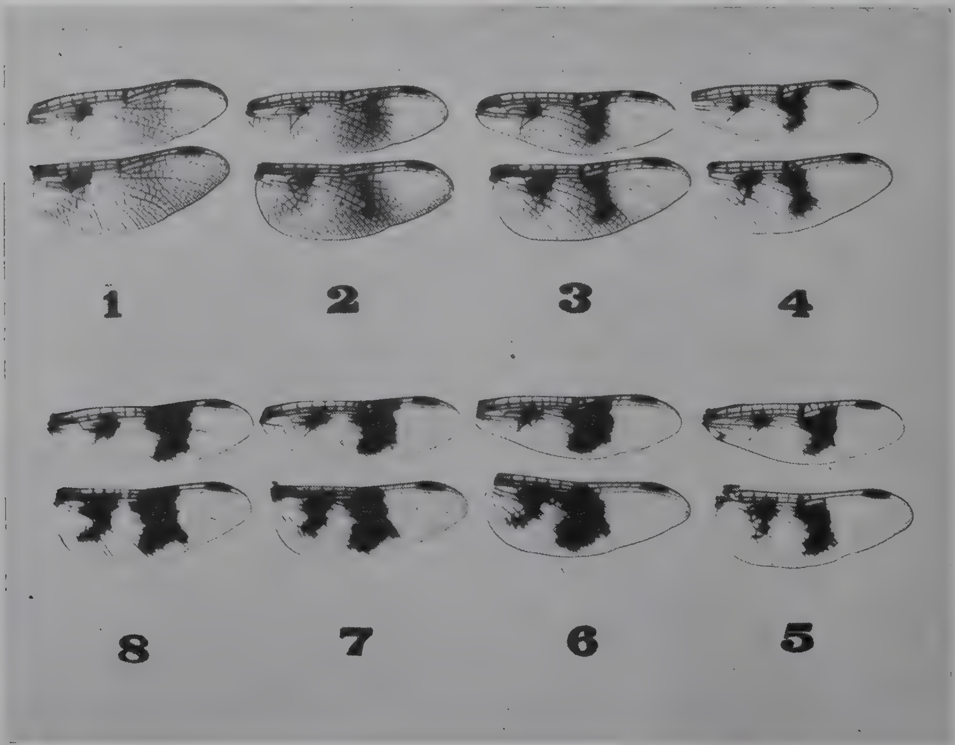

FIG. 7. Wings of Perithemis females classed according to degree of pigmentation. Classes 1-3 are light, class 4 is intermediate, and classes 5-8 are dark. The frequency distribution of color classes is as follows:

Classes:	1	2	3	4	5	6	7	8
Number:	24	157	327	344	287	259	79	20

sexes tended to select log or stick sites, while light ones tended to select patches of Potamogeton. On August 3, further observations were begun at Wiley Lake. Fourteen sites were placed at 5 m. intervals along the east bank. The sites consisted of logs charred by fire (which seemed to be especially attractive) alternating with patches of Potamogeton floated on small boards and almost sunk. All other oviposition sites were removed.

Standards were prepared by placing the wings of females between glass plates. Females were classed eight ways (Fig. 7) according to extent and density of wing pigmentation as correlated with density of body pigmentation. Males were classed three ways as before. Observations were continued until September 14. It was again found that dark forms of both sexes selected mostly logs and sticks for mating and oviposition, light forms mostly patches, and intermediate ones showed intermediacy in selection.

Further studies were conducted at the excavated pond from June 5 to July 19, 1953. Six sites similar to those studied at Wiley Lake were placed along the east bank. Only two males were permitted to remain at the studied sites at one time. Other males were caught each day as they began examination of the sites and were confined in jars containing fresh grass as perches and were kept in bags in shade. Males survived well under these conditions and were released in the evenings. In this way most of the males were prevented from localizing at a site. It was thought that this procedure might allow fuller expression of any tendency toward localization at a specific site. Females were studied according to methods employed at Wiley Lake.

The results agreed with those obtained at Wiley Lake in that a large proportion of the dark forms and a smaller proportion of the light forms selected logs, and the intermediate ones showed intermediacy in selection. Tables V and VI give a summary of the Wiley Lake and excavated-pond studies. The differences in proportions of color forms of both sexes showing differential selection of sites are highly significant.

Among those males which were captured when they arrived at the sites, only 63% of the returns were at sites visited previously, while non-captured males showed almost absolute localization to a specific site at the pond. Although the uncaptured males had much more opportunity to linger about the sites than did captured ones, both groups showed about equal tendency to select log or patch sites.

Discussion and Supplementary Observations

Competition and Sex Recognition among Males. Dashes of males at one another, pursuit displays, dual flights in Plathemis, and wing-fluttering and pursuit flights in Perithemis seem to be forms of male competition. The white upper surface of the abdomen of Plathemis and the amber color of the wings of Perithemis appear to be employed in this competition. The psychological motivation behind the competition remained obscure. Association of aggressive and sexual motivations seemed very close, for when the upper surface of the abdomen of Plathemis females is painted white so as to resemble that of a male, males dash at them as they do at other males, but this may end in copulation when the female flies.

It appeared obvious that males of both species were able to distinguish sex, for males often made only short dashes at passing males, but undertook full pursuit when a female passed at about the same distance. Plathemis males often remained motionless when other males flew overhead in dual flights, but would intercept a female flying through the air at about the same distance. Groups of many males sometimes pursued a single

Table V. *Results of site selection studies of Perithemis females. Classes 1-3 are light, class 4 is intermediate, and classes 5-8 are dark*

Observed Values

Classes	Log Selectors	Non-log Selectors	Total
1-3	200	308	508
4	185	159	344
5-8	376	269	645
Total	761	736	1497

Expected Values

Classes	Log Selectors	Non-log Selectors	Total
1-3	258.27	249.73	508.00
4	174.89	169.11	344.00
5-8	327.92	317.08	645.00
Total	761.08	735.92	1497.00

Chi-square

Classes	Log Selectors	Non-log Selectors	Total
1-3	13.15	13.60	26.75
4	0.58	0.60	1.18
5-8	7.05	7.29	14.34
Total	....	....	42.27

TABLE VI. *Results of site selection studies of Perithemis males. Class 1 is light, class 2 is intermediate, and class 3 is dark*

Observed Values

Classes	Log Selectors	Non-log Selectors	Total
1	297	375	672
2	179	186	365
3	211	114	325
Total	687	675	1362

Expected Values

Classes	Log Selectors	Non-log Selectors	Total
1	339.36	332.64	672.00
2	184.33	180.67	365.00
3	164.13	160.87	325.00
Total	687.81	674.19	1362.00

Chi-square

Classes	Log Selectors	Non-log Selectors	Total
1	5.29	5.54	10.83
2	1.54	1.57	3.11
3	13.35	13.67	27.02
Total	....	....	40.96

female. Flight pattern may be partly responsible for sex recognition. In addition, the experiments with male and female Perithemis specimens glued to sticks made it appear that that dragonfly can recognize sex of even a dead specimen on the basis of wing-color pattern.

Sex discrimination sometimes appeared obscure during periods of intense mating activity, for male-by-male coupling might then result. Perithemis males often pounce on perching males without making coupling motions: in intense competition over females, however, male-by-male coupling sometimes resulted. Similar results were obtained with glued specimens when a male would couple with a glued male after a female which he had been courting had escaped.

Moore (1952a), in his studies of British dragonflies, postulates that the species he studied were unable to distinguish sex, and he was disinclined to view the inter-male reactions of dragonflies as forms of aggressive behavior, but considered them to be results of sexual attraction between males. This opinion was based on results of experiments with males tied to strings and held in the presence of free males, which sometimes coupled with the captive. Male guarding of the ovipositing female was interpreted as follows: The ovipositing female provides the male with an attractive stimulus. Passing males also present an attractive stimulus causing the male to dash at the intruder with sexual motive. If the intruder flies away, the male returns to the stimulus provided by the ovipositing female.

In the present study it was found that when male competition was very intense, the guarding male stayed unusually close to the female. This action can hardly be explained in terms of attraction to other males.

Localization. Under ordinary conditions, some males show nearly absolute localization to one sector of the pond throughout their adult life; and since they eliminated other males from their areas (whether the motive was sexual or aggressive) the species studied show conventional territorial behavior.

Speculations on the so-called territories of dragonflies have led to three interpretations: (1) The inter-male combat may lead to sexual isolation. (2) A territory may provide a male with a hunting ground. (3) Spacing males may insure dispersal.

Williamson (1906) considered male combat to be important in sexual isolation. He postulated that males show little discrimination for females of other species, but inter-species mating is prevented by "fighting" of males for females. In the present study, male interaction was almost entirely intraspecific. Plathemis males discriminate between their females and those of other species. Females of *Libellula pulchella,* which appear similar to Plathemis females, were common at the pond, but only one coupling (without copulation) between a Plathemis male and an *L. pulchella* female was observed. Plathemis males frequently chased *L. pulchella* females, but gave up the chase on close approach. Perithemis males showed almost no attraction to females of other species, but occasionally would pounce briefly on ovipositing Plathemis females, which are much larger than females of their own species.

Saint-Quentin (1934) considered the territory or "Jagdrevier" of the dragonfly to be a hunting ground. In the present study dragonflies were only rarely observed to feed at the pond, and mating seemed to be the primary, if not only, reason for their presence at the pond.

Moore (1952a) considered dispersal to be the function of the "so-called territories" of dragonflies. He postulated that sexual attraction, resulting in clashes, caused wandering of males to bring about dispersal. Moore maintains that dispersal is not significant in preventing male interference with ovipositing females since dispersal "does not prevent interference, and therefore cannot have this function."

Although male interaction may help distribute males, prevention of male interference with ovipositing females seemed to the present writer to be an obvious function of the dispersal. This view is similar to that stressed by Armstrong (1947) in connection with arena display in birds. Armstrong maintains that this form of territorialism is an adaptation to meet the problem of a differential sex ratio. With dragonflies, this differential sex ratio is occasioned by the tendency of males more than females to aggregate at the pond. The presence of several males seriously interferes with oviposition, sometimes preventing it entirely. Spacing and elimination of males greatly alleviates this condition.

Evidence in support of this last statement was obtained from studies of the damselfly, *Enallagma aspersum* Hagen, a species in which the male retains his hold on the female during oviposition. In this species, localization at the pond was only transitory among 488 individually marked males. These males showed little interaction, but flocked close together at times. It seemed that, since the male retained his hold on the female, thereby preventing clasping by another male, territorialism is not of great advantage. Males were often observed assuming the coupling position on an ovipositing female held by another male, but oviposition seemed little disturbed. At certain times, however, the females descend stems of Potamogeton and oviposit farther beneath the water. The male then releases the female while his wings are still above the water, perches or hovers over the spot where the female descended, and shows territorial behavior in dashing at other males entering the area. When the female arises after 5-25 min. she may get caught in the surface film. The waiting male seizes her, lifting her from the water, and the pair flies away and may continue oviposition.

Sex Ratio. If the apparent excess of males at the pond lowers the biotic potential of the species by inhibiting ovipositon, the question arises as to why the ratio is not otherwise adjusted. Indications are that emerging Plathemis females already outnumber the males by about 1.62:1. Borror (1934) found among 830 individuals of *Argia moesta* that females outnumbered males by 2:1. Garman (1917) notes that female dragonflies are more easily reared than males; they may therefore be more viable. Breeding experiments with other insects would make it appear that sex ratio can be altered by genetical means.

But it may be disadvantageous for too few males to be produced, for the following advantages for an excess of males in the breeding area may be postulated: (1) Inhibition of oviposition by excess males may prevent crowding of eggs or young. (Eggs clustered in vials often failed to hatch.) Competing males may drive females from attractive sites to cause them to lay eggs on sites less attractive but in the long run more favorable. (2) With many males present, defective males may be prevented from leaving progeny. Males with defective wing tips such as result from improper emergence had very low mating scores and appeared unable to defend a territory for an extended period. This defect is probably not genetical, however. (3) Competition may preserve genetical variability by inducing frequent changing of males. (4) Frequent replacement of males at sites may be necessary for complete insemination of females. There was lowered hatching of eggs in samples taken from females when many males had been removed from the pond.

Simulation of Oviposition. Males often simulate oviposition when guarding or examining a site or following the seizure of the guarded female by another male. This activity may have the following significance: (1) It may indicate to other males that a specific site is being guarded. Males in the same area reacted toward one another less violently if each were guarding a different site than they did when both were guarding the same site. (2) It may prevent predation of the female. Perithemis males were sometimes caught by predators while simulating oviposition at the site. If other males are not numerous, his place may not be taken for hours. Females will then not likely suffer the same predation, for remaining males will attract the females to other sites. (3) The activity may be involved in the examination of a site. This is supported by the fact that simulation of oviposition occurs mostly when a male first arrives at a site.

Moore (1952b) observed simulation of oviposition among male dragonflies and interpreted the activity as a displacement reaction, that is a substitutional action of inappropriate nature following frustration of a normal action.

Differential Selection of Sites. If the tendency of dark forms of Perithemis to select logs for mating and oviposition while light ones select mostly patches of Potamogeton covered with algae has a genetic basis, it may serve as a genetical isolating mechanism. It may be important, in view of the temporary nature of some of the situations in which Perithemis breeds, that forms selecting mostly Potamogeton (perhaps open pond forms) not be strictly isolated from stick- or log-selecting forms, which may normally occupy shaded habitats where Potamogeton and algae are scarce. In the words of Dobzhansky (1951) "Too early and too rigid isolation of favorable gene combinations . . . would mean too much specialization of the organism to environmental conditions that may be only temporary." Differential site selection may bring together males and females of similar type, while inter-male competition induces mixed matings. Courtship may be related to site selection, for the male's "waiting" during courtship may allow the female opportunity to examine the site without interference.

Comparison of Color Forms of Perithemis. Comparative study suggests that the amber color in the wings of males and light females results from diffusion through the wing of dark pigment characteristic of the two patches on the wings of dark females. Light Indiana females and some males of the dark species *P. seminole* from Florida show remnants of the outer patch characteristic of dark females. The outer patch seems to disappear first, then the inner one, and finally a small spot of the inner patch, a spot found surmounting the triangle in some males. On one individual the wings of the right side were like those of a light male, whereas those on the left side showed remnants of female-like patches. This specimen was several times caught by another male before it was netted. The genitalia did not appear different from those of an ordinary male, and many sperm were being produced.

Brimley (1903) reports that tenerals of Perithemis fly in upland fields, often resting on flowers of ox-eye daisies. In this connection it is interesting that light females are inconspicuous against a background of daisies, while dark forms stand out boldly. In view of the fact that birds prey on tenerals, light forms may have a selective advantage in a pasture-pond environment.

SUMMARY

The problems of territorialism and sexual selection were studied among marked individuals of *Plathemis lydia* and *Perithemis tenera,* at ponds near Bloomington, Indiana.

The results with Plathemis were as follows:

1. The sex ratio of marked tenerals was 129 males: 209 females. Teneral males closely resemble females in color, but upon returning to the pond after the maturation period, males differ strikingly from females in having developed a bluish-brown, bluish-white, or white upper abdominal color.

2. Males examine oviposition sites and establish themselves in restricted areas near these sites which they defend against other males.

3. Males were not observed to display to females, but they appear to hide the white upper abdominal surface by lowering the abdomen while approaching females for capture.

4. Copulation time was about 3 sec. and remarkably constant, but the time was prolonged if the pair was molested by other males.

5. After copulation, the male usually places the female near the oviposition site and guards her by hovering over her while making dashes at intruding males as the female oviposits. A male may mate with and guard several ovipositing females. In all observed cases, guarding behavior was preceded by copulation with the female being guarded, or with another female at about the same time.

6. Male defence activities consisted in dashing at other males, while displaying the white upper surface of the abdomen, and in performing dual flights with other males back and forth across the pond and adjacent fields. This activity appeared partly responsible for continuous displacement of males throughout the day, and led to the establishing of territories with lateral dimensions of about 11 m.

7. There was considerable disparity in number of matings occurring at various sites, and male interaction was greater at sites much used for oviposition. Males most in evidence at 2-3 P.M. (CDT), when most mating occurred, had higher mating scores than other males.

8. When males seize ovipositing females, the guarding male becomes intensely active in dashing at nearby males and at the female placed at the site (after copulation) by the male which seized her. A mass chase of the female may result to make oviposition temporarily difficult or impossible. The female may avoid repeated seizure by remaining motionless on the site. (Males appeared to be unable to see the female in these cases and sometimes made coupling motions on the female's shadow or wing spots.)

9. Immature males fly in a slower, more fluttering manner than older males and may temporarily chase males of *Anax junius* as if mistaking them for females of their own species. They quickly seize females of their own species, but sometimes make abortive copulations. They are less active in guarding ovipositing females than are older males and are easily driven from the pond by the latter.

10. Upon return to the pond, males usually re-

turned to the areas they had occupied previously, thus showing localization. Immature males showed little localization when numerous males were present, but localization was usually firmly established by the fifth day at the pond. Localization is correlated with the development of whiteness of the upper surface of the abdomen and increasing encystment of the testes and spermiogenesis.

11. Females are captured in the air, or in the vicinity of oviposition sites when they flit around the sites or perform oviposition motions thereon. They are more easily captured by males near some sites than they are at others. Returing females showed a tendency to oviposit at sites at which they had previously oviposited even after several days' absence from the pond.

12. Females are attracted to other flying or ovipositing females, the tendency leading to communal oviposition. They never followed mature Plathemis males, but, rarely, followed immature ones.

13. When many males were removed from the pond, the remaining ones mated much more frequently than usual, but became less active after having mated twenty or more times and were easily driven away by other males. Egg samples taken at these times showed lowered hatching.

14. When all males were removed from the pond, females flitted around the sites and performed oviposition motions thereon, then became very active in chasing other dragonflies. In these cases, females performed dual flights with one another much as do males, after which one or other female would leave the pond.

15. Males with the white upper surface of the abdomen painted black were less able to defend territories and had lower mating scores than males with the surface painted white or left unpainted. The blackened males "aggregated" in sectors where relatively few matings occurred and showed a tendency to remain longer at the pond in the evenings than other males.

16. When the upper abdominal surface of females was painted white, males sometimes displayed to them as they do to other males, but they usually captured the females and mated, then, after copulation, the guarding male would fly toward the whitened ovipositing female and, when she flew, would seize her and copulate again. Guarding males would also dash at inanimate white objects.

The results with Perithemis were as follows:

1. Males precede females at the pond and closely approach projecting sticks and logs and patches of Potamogeton partly covered with algae. They then fly about a particular site and defend it against other males: finally, having eliminated male competition, they perch near the site. When a female flies over the pond, the male approaches her, then he flies slowly back to the site while the female follows. The male then hovers closely over the site as the female approaches. If the female slows down or stops, the male seizes her.

2. Copulation time was usually about 17 sec., but was greatly prolonged in shade or when the copulating pair was molested.

3. After copulation, the male flies slowly to the site while the female follows. Oviposition usually occurs at the spot where courting had occurred and particularly where the female had dipped her abdomen during courtship. If the female is chased from the site, the male follows her and leads her back.

4. If not ousted by other males, the male stays at one site throughout the day and returns to it on succeeding days with little or no re-examination. Daily arrival time of some males was quite constant and differed from male to male.

5. Male defence activity consisted in "dancing" up and down over the site, wing-fluttering near other males, and pursuit flights over the pond. A group of males "dancing" over the site resembled a swarm of "dancing" male Diptera. Defense activity led to the establishment of territories with lateral dimensions of about 6 m. There was usually complete displacement of localized males in the forenoon and another in the afternoon.

6. Males sometimes held sites where females consistently deserted them during courtship. Such males examined the sites repeatedly and flew to other sites from time to time only to be driven away by the male occupants. Males repeatedly unsuccessful in obtaining a site fly readily when dashed at by other males; the flight, being straight, like that of a female, seemed to induce male pursuit.

7. Male competition often made oviposition impossible, whereupon the female would leave the pond, perch, or fly to another site.

8. Males examining sites were sometimes preyed upon, whereupon the site was left temporarily vacant. In these cases, females are not likely to suffer the same predation, for remaining males attract them to other sites.

9. Attraction of females to other females leads to communal oviposition. With all males removed, the females may leave the pond after visiting the sites, or may oviposit alone. Of 123 egg samples obtained after females had begun oviposition alone, all contained fertile eggs.

10. Upon returning to the pond after the first oviposition, females showed a marked tendency to re-visit the previous site. Females showed a peak of repeating after an interval of one day following the first oviposition.

11. With most males removed, the remaining males mated repeatedly, then often made abortive copulations and appeared weak. Under these conditions, females were observed to fly toward perching males and pounce on them. Egg samples under these conditions showed lowered fertility.

12. In spite of wide fluctations in air temperature, the mean number of daily matings was relatively constant. On days with maximum temperatures of 33° C. or higher, there was a mating lull from 1-3 P.M. Peaks in mating often preceded a storm, during hot, humid, cloudy weather, and after unfavorable weather.

13. Males with the amber color of the wings obscured with black shoe dye were unsuccessful in competing for sites with normal males and males with the wings weighted with thinned varnish. Blackened and, to a lesser extent, varnished males were courted as females by other males.

14. When live or dead male and female specimens were glued by their feet to sticks and placed near the sites, free males pounced on the wings of glued males without bending their abdomen into the coupling position, but they quickly coupled with glued females.

15. Some males at the pond had much higher mating scores than others. The disparity of mating seemed to depend on female choice of oviposition sites. Quantitative data showed dark forms of both sexes tended to select mostly sticks and logs for mating and oviposition, light forms mostly patches of Potamogeton covered with algae, while intermediate forms showed intermediacy in selection.

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SOME POLLEN PROFILES FROM ARCTIC ALASKA[1]

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Introduction

During paleolimnologic investigations in arctic Alaska, 20 cores were taken from lakes and ponds between Fairbanks and the Arctic Ocean. Five cores, from the central part of the Brooks Range, have been analyzed for pollen and the results form the basis of this paper.

Relatively little work has been done by pollen analysts in the American Arctic. Iversen has analyzed a short core from the Mackenzie delta (Porsild 1938) and a number of long cores from Greenland (Iversen 1934, 1950, 1952-53). Hansen has examined many cores from the Yukon basin but he was concerned only with arboreal pollen (Hansen 1953). Heusser (1952, 1953, 1954) has treated the muskegs of southeast Alaska much more completely, but this region is floristically (Hultén 1941) and climatically temperate. Wenner's (1947) work in Labrador dealt mostly with the sub-arctic region.

In short, very little pollen analytic evidence is available concerning the history of arctic American Pleistocene vegetation. This is to be regretted from the point of view of the biogeographer, because many of the more interesting problems of the biogeography of northern regions (Hultén 1937, Fernald 1925) would be easily settled by stratigraphic evidence. It is also to be regretted from the point of view of the paleoclimatologist. The nature of the Pleistocene weather systems will never be understood so long as data are available only from the temperate zone.

Geography

The part of Alaska that lies north of the Arctic Circle is physiographically and botanically very diverse. It is dominated by the Brooks Range, a massive mountain chain which represents the northwestern extension of the Rocky Mountains. North and south of this range, which trends in a general east-west direction and rises to a height of some 10,000 feet (3000 m.), there lie foothill belts of lower and structurally less complex mountains. Beyond the foothills to the south of the Brooks Range is the Yukon-Tanana basin of interior Alaska and beyond the foothills north of the range lies the Arctic Coastal Plain.

Most of the Yukon-Tanana basin and the Arctic Coastal Plain shows no evidence of glaciation (Capps 1932). The Brooks Range, on the other hand, was the scene of an intensive local glaciation during the Pleistocene and supports a number of small cirque glaciers at the present day (Péwé, *et al.* 1953). Four glacial advances have been recognized, but their correlation with other glaciations is still a matter of doubt.

All of arctic Alaska, except small patches under rivers or lakes too shallow to freeze solid in winter, is underlain by perennially frozen ground. On the north side of the Brooks Range, the frozen ground extends down many hundreds of meters and only the upper half meter or so thaws out in summer.

The Yukon-Tanana basin is covered by a *Picea glauca-Betula* forest (Hultén 1941) which extends up the river valleys into the Brooks Range. *Pinus* is not present in any part of the area under discussion. In the headwater regions, progressively less of the land surface is covered by forest, and more by tundra, so that the vegetation of the foothills to the south and of the south slopes of the Brooks Range may appropriately be included under the term hemiarctic, which has been coined by Rousseau (1952) to describe a corresponding region in northern Québec. In the central part of the range, the part in which this study was located, *Picea glauca* does not reach quite to the divide. In the eastern part, there are local stands of *Populus* in some of the foothills river valleys and along the major rivers of the foothills to the north, such as the Colville, there are willows of

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[1] All field work and much of the laboratory work was supported by Contract SAR-NONR/340(00) between Yale University and the Office of Naval Research of the United States Navy. Analysis of the cores was completed during tenure of a National Research Council of Canada Post-doctorate Overseas Fellowship at Cambridge University. Most of the data presented in this paper formed part of a thesis presented to the Department of Zoology, Yale University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Headquarters for the field work was the Arctic Research Laboratory, Point Barrow. The author is indebted to Dr. Ira Wiggins and his staff at that laboratory for logistic support, to Mr. Kirk Bryan, Jr., and Mr. Richard Leahy for assistance with the field work, and to Prof. G. E. Hutchinson, Mr. Heikki Ignatius, Dr. Richard West, Miss R. Andrew, Dr. Harry Godwin and Dr. Johs. Iversen for much stimulating discussion. Grateful thanks are extended to Dr. E. S. Deevey, Jr., who supervised the work at Yale and provided friendly aid and criticism throughout the investigation.

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tree size. Otherwise the north slope of the mountains and the plain beyond are completely treeless.

The terms arctic, subarctic, and hemiarctic will be used in this paper to describe the Alaskan climate and vegetation. 'Arctic' will refer to places where the winters are cold and the summers too cool for tree growth. 'Subarctic' will refer to places where the winters are cold but the summers are warm enough to permit a more or less continuous growth of forest. 'Hemiarctic' will describe the zone between the arctic and subarctic where the balance is so delicate that microclimatic factors govern the distribution of forest. The vegetation here is a patchwork of forest and tundra.

Weather stations are extremely scarce and there are no official data for Death Valley and Chandler Lake, the sites of the analyzed profiles. Synoptic data for two stations are presented in Table I.

Table I. *Mean weather data for at least five years from two stations in arctic Alaska (U. S. Weather Bureau 1943). Temperatures are in °C. and precipitation in cm.*

Location		Mean temperature	Mean max. temperature	Mean min. temperature	Mean precipitation
	July......	4	8	1	2.3
Pt. Barrow	January...	−27	−24	−30	0.5
	Annual....	−12	− 9	−16	10.7
	July......	12	20	7	3.8
Wiseman	January...	−24	−19	−30	1.5
	Annual....	− 6	0	−12	22.4

Wiseman is located in the Upper Koyukuk Valley, about 50 km. from Death Valley. The weather in the two localities is probably very similar. No data are available from any station which is really comparable with Chandler Lake. It is about 140 km. from Wiseman, but on the other side of the mountains. Probably its weather is intermediate between that of Wiseman and Point Barrow. During the field work at Chandler Lake, the weather was a little wetter and a little warmer than at Point Barrow, and the winds much stronger. The Climatic Atlas for Alaska (U.S. Weather Bureau 1943) estimates the mean annual temperature of the north slope generally at −9 to −10°C. and the annual precipitation at about 18 cm. Details may be lacking but the main features of the climate are clear: the precipitation is low, the summers cool, and the winters cold.

Methods

The localities from which the material for pollen analysis was obtained lie in a remote and uninhabited region accessible only by bush plane. This imposed severe weight restrictions upon the apparatus to be used. One core was taken with a modified Hiller sampler equipped with removable liners and the other 4 were taken with a sampler of original design which has been described in a separate publication (Livingstone 1954). Aluminum alloy extension rod of the type designed by Lichtwardt (1952) was used with both samplers. Inflatable six-man rubber dinghies provided drilling platforms.

Preparation of the samples was carried out by the bromoform method of Frey (1951), followed by the acetolysis method of Erdtman as described by Faegri and Iversen (1950). The pollen was mounted in glycerine jelly containing safranin and counted at a magnification of 430x. An oil immersion objective (1/12) was used for difficult grains.

Because of inexperience and the lack of a complete reference collection of Alaskan pollen types, it was not possible to identify all grains. Unknown grains or ones too badly crushed for identification usually amounted to around 5 per cent of the total pollen, but occasionally rose to 25 per cent. It is hoped that many of the unfamiliar grains will be identified as investigation of the Pleistocene history of northern Alaska continues.

Mr. John McClymont of the University of Michigan Botany Department very kindly examined some of the slides and verified the presence of moss spores. None of the kinds was distinctive enough to permit identification beyond Bryophyta. It is, however, quite possible that similar fossils of unknown origin may have been combined with moss spores in the counts.

Results

Pollen diagrams have been constructed for four localities in the central Brooks Range (see map, Figure 1). They are from Chandler Lake, on the north side of the divide, at latitude 68° 15′ N., longitude 152° 42′ W.; Eight Lake (author's name), a few miles south of Chandler Lake, at latitude 68° 8′ N., longitude 152° 50′ W.; Lake A, a few miles north of Chandler Lake, at latitude 68° 21′ N., longitude 152° 39′ W., and a small lake in the valley of the Wild River, on the southern edge of the Brooks Range, about 20 miles north of Bettles. This last lake is located at latitude 67° 10′ N., longitude 151° 25′ W., near Chicken Creek and opposite the place where Death Valley Creek joins the Wild River. It will be referred to as the Death Valley station, the other three as the Chandler Lake, Eight Lake and Lake A stations, respectively.

Chandler Lake Region

Chandler Lake lies in the glaciated U-shaped valley of the Chandler River. It is the largest of

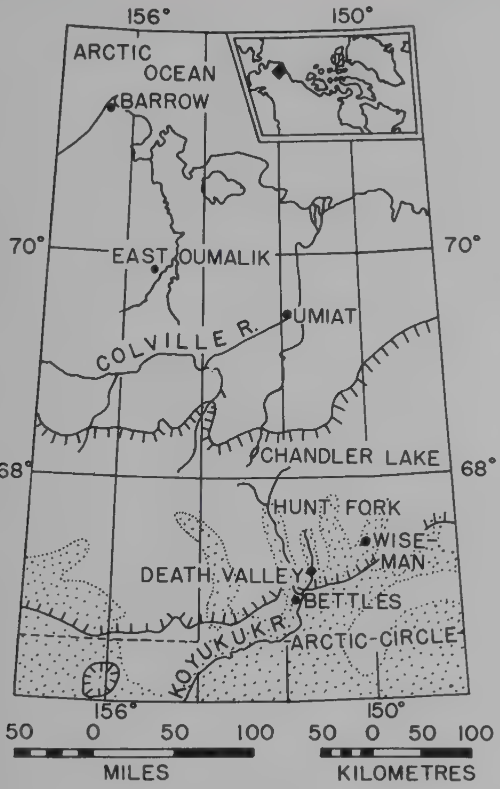

FIG. 1. Map showing the localities described in the text. The hachured line shows the approximate boundary of the Brooks Range glaciation (after the Glacial Map of North America). The stippling shows the approximate extent of the *Picea-Betula* forest (after Hultén 1941-50).

several lakes lying behind a series of moraines and seems to owe its origin partly to glacial scouring of the valley floor and partly to the damming action of the moraine at its downstream end.

The lake lies at an altitude of some 1950 m. (2900′) and the mountains which surround it rise to 2500 m. (7500′), according to the U. S. Geological Survey Alaska Reconnaissance Series, Chandler Lake Sheet. There are no trees in the vicinity. The vegetation is dominated by sedges and grasses, although dwarf birches are common and shoulder-high thickets of willows grow along some of the tributary streams. Ericaceous shrubs, particularly *Ledum palustre* and *Cassiope tetragona,* are fairly common, as are a number of flowering herbs. The nearest known spruce trees are a few outliers which grow along the valley of the John River to Hunt Fork, 50 km. (30 miles) away. Alder bushes grow at Umiat, 130 km. (80 miles) to the north, in the valley of the Colville River, and probably grow much closer to Chandler Lake in other sheltered localities. It is probable that on the John River drainage alder grows at least as near as spruce.

Till-bodies of two very different ages are found in the vicinity. The older till lies to the north of Chandler Lake and the other lakes along the Chandler River. It appears to be a very massive body, reaching a height of some 100 m. (300′) above the valley floor, but it is impossible to tell, in the absence of subsurface data, how much of its bulk is actually composed of till and how much of outwash or bedrock.

It extends along the flank of the Brooks Range as far as one can see on a clear day and quite far to the north, no doubt grading into outwash northward. Large conglomerate boulders were seen on the ground for 21 km. (13 miles) north of Chandler Lake, far from the nearest outcrop of conglomerate bedrock. From the air, boulder gravel was seen as far north as Castle Mountain, 37 km. (23 miles) from Chandler Lake, but this exposure was not examined on the ground.

The surface of this till-body has been much modified since deglaciation. A considerable thickness of oxidized flow earth has accumulated on its surface, about 1.6 m. (5′) being exposed in slump scars. The creep by which this flow earth was deposited in the swales has smoothed the contours of the ground, so that kames are hardly recognizable and kettles are much modified.

A small proportion, perhaps a few per cent, of the stones on the surface have a weathering rind of about 5 mm. (0.2″) thick. A few of the stones, especially ones of favorable rock types, are striated also. The surface of the till is well-covered with cottongrass (*Eriophorum*) tussocks and other vegetation.

It is quite possible that this till-body was laid down during a number of successive glaciations, but there are no deep exposures, and there is no surface evidence of more than one glaciation. Several small moraines on the surface of the till-body, such as the one that dams Chandler Lake, do not differ in depth of weathering or topography from the main part of the till, and it seems most likely that they are recessional moraines formed during minor readvances of the ice sheet that formed the main till-body.

The second till has been examined at only one place, a few miles south of Chandler Lake on the side of the main valley, but it probably occurs up the other valleys as well. Lateral moraines which may be of the same age were seen from the air in a number of these side valleys.

This till is obviously much younger than the one that lies to the north. Its surface is of an unmodified kame-and-kettle topography. Vegetation is almost absent, except in the swales. There is very little flow earth accumulated at any place on the surface and no stones with weathering rinds were found. Eight Lake lies in one of the small kettles on the surface of this younger till.

The size and situation of the two till-bodies, the extent to which erosion has modified them and the size of the kettles they contain all agree in suggesting that they are to be referred to the Itkillik and Eschooka glaciations which Detterman has described from the Anaktuvuk Valley, the next major valley to the east of Chandler Lake (Péwé, *et al.* 1953). These glaciations have been tentatively correlated with ice advances on the Kenai Peninsula which occurred more than 18,000 years ago and between 8,000 and 14,000 years ago, respectively.

Descriptive stratigraphy.—Three cores from Chandler Lake have been analyzed for pollen. The first, 2.5 m. long, was used in learning the elements of pollen analysis and no reliable results have been obtained from it. The second was taken through 7 m. of deltaic deposits near the point where the Chandler River enters the lake and yielded a pollen profile without change from top to bottom. It is devoid of vegetational significance and is of interest only because it shows the rate at which deltaic deposits can be built up.

The third Chandler Lake core was taken in the center of the lake and reached to a depth of 5 m. It was taken in 19 m. of water and it was not possible to say, from the circumstances of the field work, that the bottom of the deposits had actually been reached. Indeed, the results of the pollen analysis, as will be seen presently, indicate that such was not the case.

This core (see Figure 2) established the most

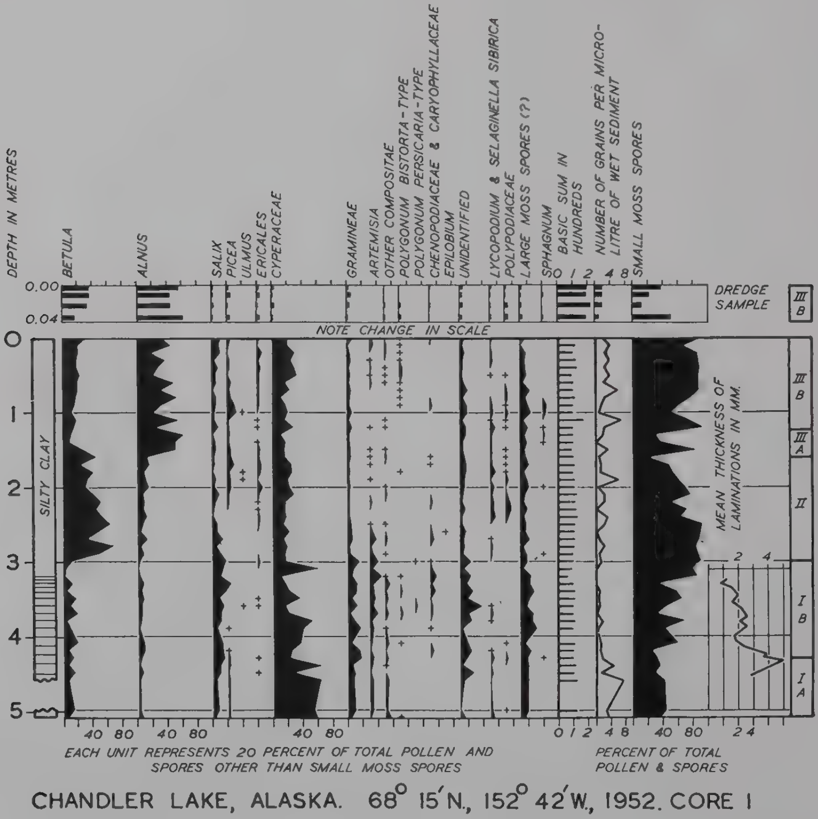

Fig. 2. Pollen diagram for Chandler Lake. The histograms in the upper part of the diagram show the results of analysis of the uppermost layers, obtained with an Ekman dredge.

complex series of vegetational changes of any so far examined from the Brooks Range. Even this series is remarkably simple when contrasted with a postglacial section from the temperate zone. The diagram can be divided with assurance into only 3 zones. From the bottom, they are an herbaceous pollen zone, a birch pollen zone, and an alder pollen zone. The herbaceous zone might be divided into 2 sub-zones, in the lower of which sedge predominates over all other kinds of herbaceous pollen, but such a division, on the basis of a single diagram, would not be very secure. There is also a slight tendency for the alder to decline in the upper part of the alder zone. This occurs in cores from 2 other sites in the vicinity as well and is probably a significant shift, but it lacks the clear-cut character associated with pollen zones and sub-zones farther south.

An interesting aspect of this core is the existence, in the herbaceous zone, of lamination in the sediment. Doubtful lamination of various kinds occurs in other parts of the core as well, particularly near the top, but only in this zone are the bands marked and regular enough to be counted and measured. At least some of the laminae appear to be graded beds, but they are much thinner (1-5 mm.) than the varves of ice-dammed lakes.

Even where conditions are very favorable, great care and experience are needed in deciding whether a given lamination is a varve or not. Ideally one seeks internal evidence of its annual nature, such as Welten (1944) found in the Faulensee deposits, before applying the term varve to any lamination. It has not been possible so far to demonstrate seasonal microfossil shifts in these graded beds. The pollen density of the sediments in so low that the complete substance of several laminae is required to provide a significant number of grains. It would not be possible to establish the annual nature of this lamination against vigorous criticism. It is very interesting, however, to assume that the laminae are varves and see to what tentative conclusions this leads.

Including a few short interpolations there are 665 laminae in the herbaceous zone. It is unlikely that they are diurnal bands, because within the laminated zone occur changes in relative pollen frequency which would occupy not hundreds of days but hundreds of years. If the choice were only between diurnal and annual bands it would be possible to say with confidence that these laminae are indeed varves. It is unfortunately true, however, that the bands may be aperiodic, and may result from heavy precipitation or very rapid thawing which occurred several times in some years and not at all in others.

If the bands are annual then the core must cover a minimum of 665 years' time. If we extrapolate the mean thickness of the bands up to the surface and down to the bottom of the core, then the period of time which it represents must be of the order of 2,400 years. If, as is much more reasonable, we take the minimum value for varve thickness, on the basis that sedimentation under the glacial conditions necessary to produce varves is much more rapid than that under ordinary circumstances, then the time represented by the core must embrace at least 3,800 years and probably much longer.

So far as it goes, this estimate does not disagree with the age, 8,000-14,000 years, arrived at by correlation of drift morphology through the Eschooka glaciation of the Anaktuvuk area to the radio-carbon-dated Naptown glaciation of the Kenai Peninsula (Péwé, *et al.* 1953). It appears very likely that the time represented by this core is, roughly, post-Mankato in terms of the drift stratigraphy of the American Middle West and postglacial in the sense of European pollen analysts.

If this diagram from Chandler Lake is compared with the diagrams from Eight Lake and Lake A (see Figures 3, 4) it will be seen that they do not possess the herbaceous zone but that the alder and birch zones are present in them. This is not surprising for Eight Lake. It lies on a till-body which is younger than the one damming Chandler Lake and so must be younger than Chandler. From the stratigraphy, it appears that the glaciation that produced Eight Lake is the same as the one that laid down the laminae in Chandler Lake. This glaciation never reached the shores of Chandler, and it is probably this circumstance which accounts for the weak development of the bands.

From the circumstances of the field work, particularly the very hard and irregular bottom which stopped the coring operation at a depth of 2 m., it seemed that the Eight Lake core ended on the rocky floor of the kettle, and that the pollen diagram for this lake should represent all of the time since the lake was formed. The same cannot be said of the cores from Chandler and Lake A. The depths of sediment and water were much deeper in these lakes, the sediments were stiffer, and the drilling operation was carried out in windy weather. All these circumstances combined to limit the depth of the cores and in both lakes drilling was terminated when the stiffness of the sediments made further progress impracticable, rather than because any hard irregular bottom was reached. On field evidence, it is extremely doubtful that

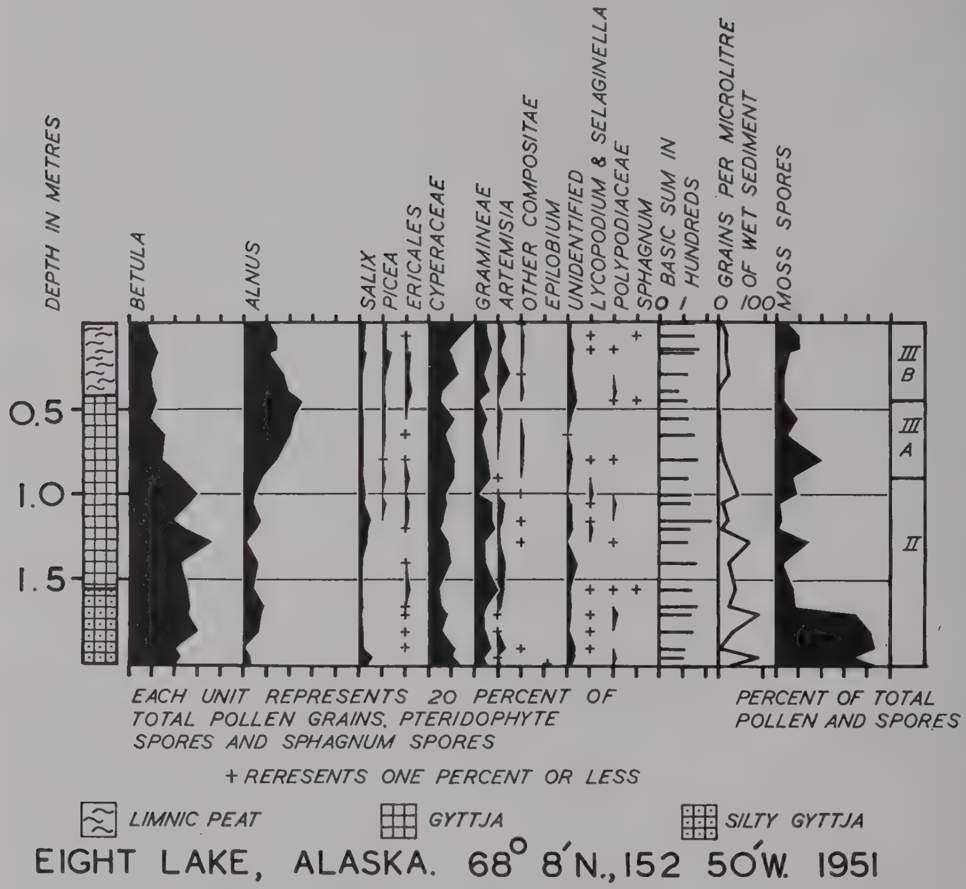

FIG. 3. Pollen diagram for Eight Lake.

the Chandler and Lake A cores represent complete sections, and this is borne out by the pollen stratigraphy. The oldest sediments sampled in Lake A seem very little if at all older than the oldest in Eight Lake, and the oldest in Chandler seem to be only half as old again or less.

There is a strong feeling among students of kettle sediments that stagnant ice blocks in till or outwash may long survive their parent glaciers, and that on this account the sedimentary record in a kettle may not account for all of postglacial time in the region. It is perhaps worth noting that Eight Lake, though it lies in a region of perennially frozen ground, does not seem to be missing very much of the postglacial record from the bottom of its sediments. With a pollen profile showing so few zones it is difficult to be sure that the core is not truncated to some extent, but it does not appear that a substantial fraction of the core is missing. The Eight Lake profile, at its bottom, does not differ radically from the Chandler Lake profile half a meter above the top of the varve sequence. Perhaps the rocky, unvegetated nature of the till-body on which Eight Lake lies made it a particularly unsuitable refrigerator for the preservation of stagnant ice.

Vegetational interpretation.—Interpretation of the pollen diagrams in terms of vegetational changes offers some difficulties.

Most of the sediments from the Brooks Range are rather inorganic and contain a high proportion of clay and silt. Material of this sort in temperate regions is very likely to contain large amounts of secondary pollen derived from the deposits which were weathered to yield the silt and clay. Lateglacial deposits in regions which contain extensive interglacial deposits often have so much of this secondary pollen that it masks the nature of the

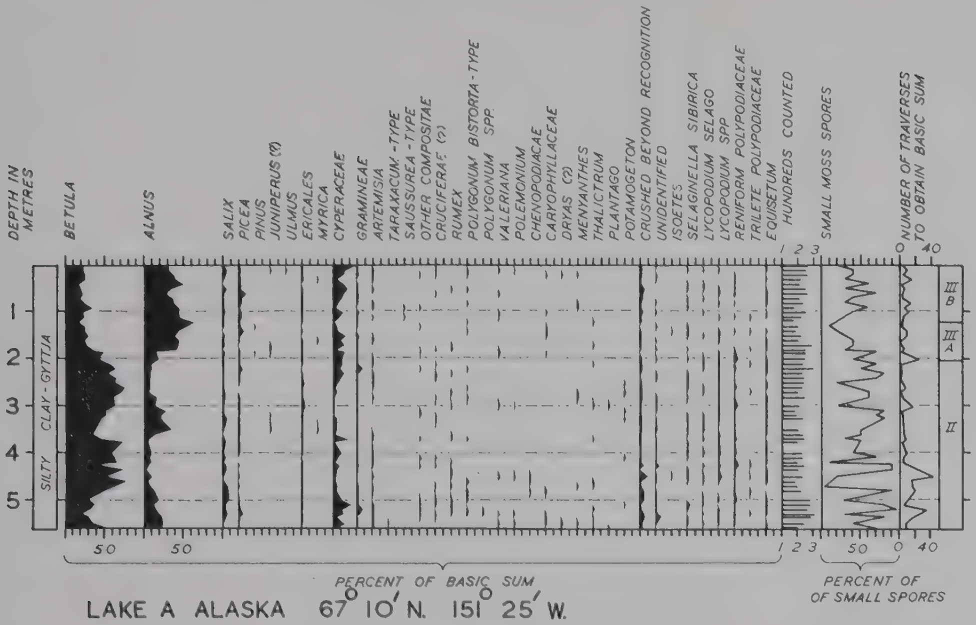

Fig. 4. Pollen diagram for Lake A.

late-glacial vegetation. For a variety of reasons, however, it does not seem likely that the Brooks Range sediments, despite their inorganic nature, contain appreciable amounts of secondary pollen. Exotic grains are very few. Two or three pine pollen grains were observed during the counting, but so small a number might be expected as a result of long-distance transport or contamination. A trace of *Ulmus* pollen was observed as well, but these were fresh, well-preserved grains. They were most abundant in slides made up during the flowering season of *Ulmus* and are believed to be contaminants introduced during preparation of the slides. No other unexpected grains were encountered.

It is quite possible that the lack of exotic grains may be due to the fact that the interglacial vegetation was rather similar to that of the present day. This, if true, is rather disquieting, for it removes the possibility of recognizing contamination if it occurs and also of applying the standard correction method (Iversen 1936).

On the other hand, if the only possible contaminating pollen is derived from tundra and park tundra deposits, it is less likely to be quantitatively important. Pollen production of open vegetation is notoriously low. If the sediments of a tundra lake are contaminated with a small volume of sediment derived from a temperate lake, then the distortion of the pollen profile will be great, because of the much higher pollen frequency of temperate lake deposits. But if the tundra lake sediments are contaminated with a small amount of sediment from an older tundra lake, then the distortion of the younger lake's profile will be very much less.

The situation of Chandler Lake and Eight Lake makes secondary deposition unlikely. They are surrounded by rocky talus-clad mountains and most of the mineral sediment that reaches them appears to be derived by weathering from the Paleozoic rocks of these mountains. The small till-body of the Eight Lake glaciation has hardly been eroded at all. It is very rocky and seems to consist mainly of rock debris scraped off the mountain sides by the Eight Lake glacier. It seems a most unlikely source of serious contamination.

Lake A is rather different. It lies in a very massive moraine which is not nearly so rocky as that at Eight Lake, and it must include in its substance whatever lake sediments lay in the preglacial Chandler Valley. It is obvious from the topography of this moraine that a very considerable body of till has been redeposited in its kettles by mudflow and creep, and it would not be at all surprising to find that secondary deposition had occurred here on a seriously large scale.

General correspondence of the Lake A profile with the Chandler Lake and Eight Lake profiles shows that the amount of such contamination, if it has occurred, was not sufficient to mask the vegetational changes. The persistence of a small amount of spruce pollen throughout the profile, while it was absent from part of the other two, suggests that some secondary deposition may have occurred.

The Death Valley Station, similarly, is one where there is no evidence of extensive redeposition, but where the possibility cannot be ruled out.

At the bottom of the Chandler Lake core lies a zone in which herbaceous plants dominate the spectra. The largest single category is sedge pollen, particularly in the lower half of the zone. It has not been possible to identify the genera involved, but the pollen is of the type which characterizes *Eriophorum, Kobresia,* and *Carex*. Probably cottongrass tussocks were even more important in the vegetation at that time than they are today.

Various other categories enter into the pollen of the herbaceous zone, particularly Gramineae, Compositae, Salix, Chenopodiaceae and Caryophyllaceae. The proportion of unidentified grains also rises to a maximum during the upper part of the herbaceous zone, as does that of moss spores. Every one of these herbaceous zone elements is characteristic of the tundra much farther north at the present day (compare the surface spectra from Point Barrow in Table II). They indicate conditions under which much fresh ground was available for colonization by herbaceous plants, presumably because of a severe climate with extensive frost-scarring of the ground. This is in accord with the presence of the glacier which formed the kettle occupied by Eight Lake.

The increase of indicators of fresh ground at the expense of sedge in the upper part of the herbaceous zone may possibly indicate the height of this minor glaciation. It may, on the other hand, simply represent conditions of deglaciation with bare ground uncovered by the retreating ice. The absolute pollen frequency favors the first of these alternative hypotheses. It is very low where the percentage of bare ground indicators is high. If the bare ground species were colonizing recently deglaciated terrain, the absolute pollen frequency ought to be higher, not lower, than in the levels immediately below. Unfortunately the lowermost sample was disturbed while it was being taken and it was not possible to determine the laminar thickness although laminae appeared to be present.

TABLE II. *Pollen spectra of mud surface samples from three lakes on the arctic slope of Alaska*

Pollen or spore type	71° 16′ N.,† 156° 39′ W. Footprint Lake near Pt. Barrow	71° 15′ N.,† 156° 37′ W. Unnamed Lake near Pt. Barrow	69° 49′ N.* 155° 25′ W. East Oumalik Lake
	Per cent of total pollen and pteridophyte spores		
Betula	7	5	13
Alnus	5	10	9
Salix	3	4	3
Picea	+	+	3
Ericales	2	—	—
Cyperaceae	36	24	25
Gramineae	41	49	18
Artemisia	—	—	1
Taraxacum-type	—	—	+
Other Compositae	+	1	—
Rumex	+	—	—
Cruciferae	—	+	2
Epilobium	+	—	—
Unidentified	1	1	2
Crushed beyond recognition	2	+	13
Lycopodium Selago	—	—	+
L. spp.	+	—	—
Polypodiaceae	—	—	2
	Per cent of total pollen and spores		
Hairy moss spores	2	1	+
Small moss spores (?)	11	19	40
Large moss spores (?)	20	32	6
Number of pollen and spores counted	267	283	333

*Sample taken by Ekman dredge.
†Sample taken by hand from the undisturbed bed of a recently drained lake.

It would be easy to overemphasize the similarity of the Chandler Lake herbaceous zone spectra with surface spectra from Point Barrow. There are, actually, some minor but significant features, such as the absence of *Artemisia* from the Point Barrow spectra. The vegetation at Point Barrow is a coastal tundra and although the sea may formerly have been much closer to Chandler Lake than it is now, a genuine coastal tundra would hardly be expected during late-Pleistocene time in the Brooks Range. The difference of substrate, too, would prevent complete parallelism of vegetation in the two areas. At Point Barrow, there is a deep mantle of finely divided material, while around Chandler Lake the bedrock is thinly and discontinuously covered.

Fossil vegetation can never be matched exactly by modern examples. The similarity between the herbaceous zone at Chandler Lake and the modern vegetation at Point Barrow is mentioned only as a suggestion of what the herbaceous zone vegetation may have been like. Probably there are types of high-arctic vegetation in the Canadian archipelago which would compare much more closely with the fossil vegetation of Chandler Lake.

Above the herbaceous zone lies the birch zone. So far, it has not been possible to identify the birch species of this zone from leaves or other macrofossils, but the bulk of the pollen probably comes from the dwarf birches, *Betula nana* ssp. *exilis* (Hultén 1944) and *Betula glandulosa,* rather than any of the tree birches (*B. kenaica, B. papyrifera* ssp. *occidentalis, B. resinifera*) which inhabit the warmer parts of Alaska. Spruce is much scarcer in the lower part of the birch zone than in the alder zone, and *Lycopodium* and ferns are absent from the lowermost part of the birch zone as well. It would be difficult to imagine one element of the interior forest, the birches, spreading over the north slope without taking along the spruces, ferns and *Lycopodium* which are such prominent components of the interior vegetation.

Further, alder is intermediate in thermophily between open tundra and tree birches. It would be unusual, to say the least, for the vegetation to pass from the obvious tundra of the herbaceous zone to birch forest without passing through at least a short phase in which alder was an important pollen constituent. As Figure 2 shows, alder is virtually absent at the the transition between birch and herbaceous pollen zones.

Dwarf birches, on the other hand, are an important element in the tundra vegetation, at least as far north as East Oumalik (latitude 69° 40′ N., longitude 155° 25′ W.) although they are not present in abundance at Point Barrow on the arctic coast. They occupy, in short, a latitudinal and altitudinal belt between tundra of grasses and shrubs and tundra with local thickets of alder in the sheltered valleys. They are, of course, also present south of this belt, but their influence in the pollen rain there is diminished by the presence of other heavy pollen producers such as alder itself.

The birch zone, then, seems to represent a time when the alder thickets were too far away from Chandler Lake to influence the pollen rain markedly—a time when the climate was somewhat more severe than it is at present. The vegetation may be considered as not being too different from that of East Oumalik at the present day. The pollen spectrum of a surface dredging from East Oumalik Lake is given in Table II for comparison. Differences in topography and substrate between the two localities prevent complete parallelism, but it can be seen that this surface spectrum from East Oumalik resembles fairly closely those of the birch zone at Chandler Lake.

The next problem which arises in the interpretation of the Chandler profiles is that the uppermost zone is characterized by the dominance of alder although today no alder grows in the vicinity. Spetzman (1951), however, records alder from two other parts of the Brooks Range, Killik River 60 km. (40 miles) away, and Anaktuvuk Pass, 50 km. (30 miles) away. Alder thickets may grow even closer but it seems probable that there is not a single bush within 20 km. (12 miles) of Chandler Lake.

One possible explanation is that alder was much more widespread until very recently and that a climatic or ecological shift of the past 50 or 100 years has forced it back. There is difficulty in testing this palynologically because the uppermost sediments of a lake are usually missed with a standard pollen sampler, and the top spectrum of most cores usually dates from some time in the past few centuries.

In order to overcome this difficulty, a mud surface sample was taken with the Ekman dredge and a subsample was taken from the uppermost layers of the undisturbed dredging by pushing a metal tube into it. The water was carefully drained off, and the tube sealed in polyethylene. On return to the laboratory this sample was analyzed at close intervals. The results are shown as histograms at the top of the Chandler Lake diagram. It can be seen that there is no spectacular decline in *Alnus* frequency in the uppermost layers. The top sample may represent the summation of as much as 50 years' pollen rain, but not much more. If there had been extensive alder thickets around the lake as recently as 50 years ago, some trace of them would surely persist at the present time, for wood decays very slowly in the Arctic. No such remains were seen, although care was taken to watch for remains of former trees and bushes.

It is much more likely that the high alder pollen frequency represents moderate-distance transport by the wind. This seems extraordinary in the light of temperate zone experience, particularly in Europe, where alder has been regarded as a species of local derivation. In temperate Europe, it occurs in conjunction with extensive forest of high pollen production. The alder bushes themselves occupy wet river bottoms or carrs and are frequently found growing on the surface of the deposit which is being studied.

In northern Alaska, alder, especially *Alnus viridis,* grows beyond the tree line, or in places where the only trees are willows of low pollen productivity. Beyond the latitudinal and altitudinal limit of alder the pollen of local origin comes mostly from shrub birches, ericaceous shrubs, grasses, sedges and miscellaneous herbs. Of all these categories, none produces pollen in such great quantities as alder and none except willow sheds its pollen at so great an initial height. For these reasons, it does not take a particularly great absolute quantity of windblown pollen to figure very largely in the percentage calculations. Even at Point Barrow, at least 120 km. (75 miles) from the nearest alder bushes, alder pollen is relatively abundant in the surface samples. In short, in Alaska, alder behaves the same way as pine behaves in Lapland (Aario 1944).

Various workers (*e.g.*, Deevey 1951 : 198, Donner 1951 : 22) dealing with tundra or late-glacial vegetation have set arbitrary limits to the ratio of non-arboreal pollen to tree pollen or to the absolute pollen frequency which characterizes the change from forest to park-tundra or from park-tundra to open country. These limits are based upon a background of local experience and may be very nearly correct. The practice is an unhappy one, however, for such values, arrived at as a result of long experience in a rather circumscribed region, are apt to be taken over uncritically and applied by other workers to other localities. Such arbitrary use of the NAP/AP ratio is particularly to be regretted. If one were to calculate such a ratio in the standard way for the surface levels of the cores from the Chandler Lake region, one would arrive at the conclusion that the area was covered by some kind of birch or alder scrub or forest. In actuality, the vegetation is tundra and the element which dominates the landscape is the *Eriophorum tussock,* with more or less of included birch and heath shrubs. Throughout northern Alaska, large areas of tundra would be classified as park-tundra or forest on this basis. If one were to set up an arbitrary standard for Alaskan tundra it would involve an NAP/AP ratio much closer to ¼ than to the usual ¼.

Such arbitrary standards are very misleading and ought not to displace botanical experience and common sense in the interpretation of pollen profiles. In very many cases, the evidence will not suffice to discriminate between open and closed vegetation, and it is much better to face these uncertainties than to cloak them under a mantle of arbitrary decision. The decisions in the past have probably tended to make more imaginary forest out of actual tundra than the reverse, for there has been a feeling, particularly in America, that vegetation must be considered forest until it has been proved otherwise. This view has neither logical nor ecological merit.

It is not generally appreciated how many different vegetation types and corresponding pollen spectra are included in the term "tundra." Thus, Potzger (1953) has recently attacked Deevey's (1951) excellent work in northern Maine on the ground that his late-glacial spectra contained too much grass pollen and too few lichen spores to represent tundra. Potzger's impression of tundra appears to be based on the hemiarctic region of northern Québec (Rousseau 1952) where the vegetation of the tundra areas is dominated by a dense growth of fruticose lichens. It is interesting in this connection to look at the surface spectrum from Point Barrow (Table I), where the present vegetation is a rather common type of tundra. The Point Barrow spectrum is dominated by grass pollen.

As for the lack of lichen spores, there is nothing remarkable in that. Lichens do not appear to fossilize, and to the best of the author's knowledge have never been found in Pleistocene deposits from the Arctic or anywhere else.

To return to the consideration of the alder zone in the Chandler area, it will be seen that in all three diagrams, the last event is a slight decline in alder. This is a very minor shift, and may not be significant, even though it occurs in all three sites. Under Chandler Lake conditions *Alnus* may be taken as an indicator of warm summers and this slight decline may indicate that the climate has deteriorated very slightly after reaching a time when summer temperatures were a little higher than present ones. If this is so, it is the only trace in these diagrams of a phenomenon, the post-glacial thermal maximum, which is now known from many parts of the world, including New Zealand (Cranwell and von Post 1936) and southeast Alaska (Heusser 1953).

It is worth noting that *Picea,* which is also an indicator of warm summers under these conditions, reaches its highest values at or a little below the alder maximum in all three cores.

Death Valley Region

Death Valley Lake is the largest of number of small lakes that lie on what appears to be a pitted outwash plain just above the mouth of the Wild River. This outwash plain is confined behind a ridge of low hills, except for a single tongue which runs through the Wild River gap almost as far as the junction with the Upper Koyukuk River. South of this outwash valley there is no evidence of glaciation. North of it the Wild River Valley becomes U-shaped with truncated spurs and has obviously been glaciated. This is in accord with the observations of Capps (1932) who places the limit of the Brook Range glaciation in this area near Bettles. Death Valley Lake appears to be near the limit of a major glaciation in the area, though not necessarily the last one, nor, indeed, the most extensive. There may be evidence of a former glaciation south of the outwash

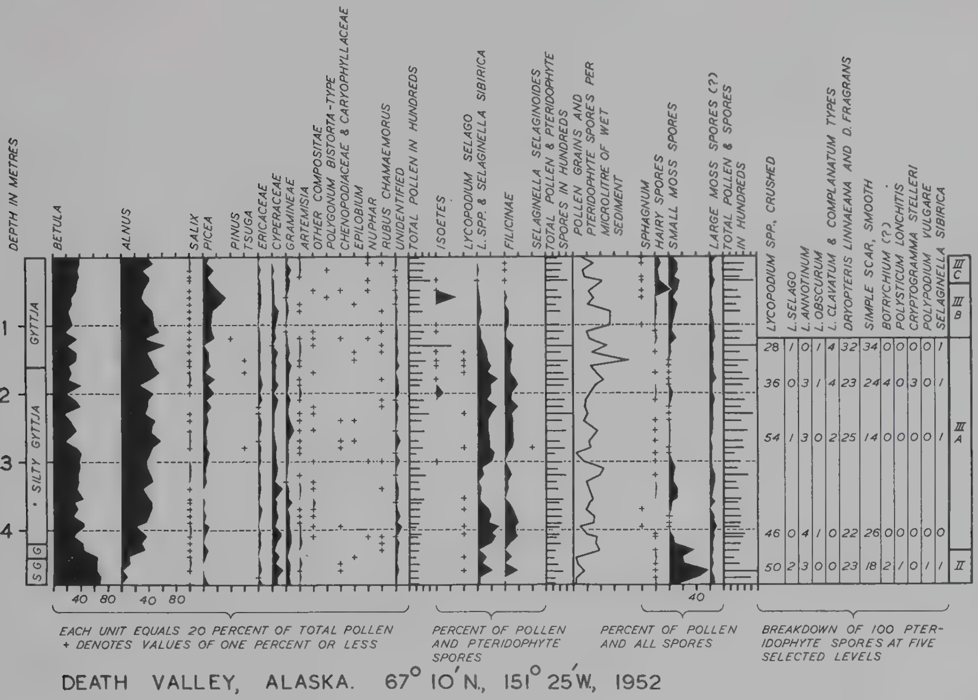

Fig. 5. Pollen diagram for Death Valley Lake.

plain which escaped the rather cursory aerial reconnaissance upon which the foregoing description is based.

It is impossible to say, in the absence of hydrographic data, whether Death Valley Lake is a thaw lake or a kettle.

Descriptive stratigraphy.—The single core from the Death Valley region begins with a *Betula* maximum (Figure 5). As birch declines, alder increases to dominate most of the profile. There is a *Picea* maximum in the upper meter, while small moss spores have two maxima, the larger at the bottom of the profile, the smaller at the top.

Vegetational interpretation.—Although the Death Valley core contains a birch and an alder zone, it would be extremely dangerous to equate them with the Chandler Lake birch and alder zones in a time sense. The Death Valley region is not arctic, despite its location north of the Arctic Circle. The protection of the Brooks Range shuts it out from the cool summers of the Arctic Coastal Plain and includes it in the climatic and vegetational region of interior Alaska. The vegetation is hemiarctic and the trees include birches, spruces and poplars at the present time.

The birch zone at the bottom of the profile suggests a cottongrass tussock tundra with many dwarf birches and some grasses and heaths. It corresponds vegetationally with the birch zone of Chandler Lake and the present vegetation of East Oumalik, but there are differences in detail. In particular, the frequency of sedges and *Lycopodium* is slightly higher at Death Valley than at the other places. The differences are maintained throughout the zone and are likely due to the greater continentality of Death Valley.

The upper levels of the pollen profile are dominated by alder with birch in the second position, so that the spectra resemble those of the Chandler Lake alder zone, but there is a slight and highly significant difference in the incidence of spruce pollen. This is a good illustration of the difficulty of recognizing the shift from tundra to park-tundra on the basis of pollen alone. It is easy enough to attach the proper significance to the difference in the spruce incidence when one knows, from having examined the vegetation, that Chandler Lake lies within the tundra and Death Valley within the region of hemiarctic vegetation, but the difference is so slight that it would probably have escaped unnoticed if it had occurred in the middle of a long profile.

The *Picea* maximum in the upper meter probably represents the post-glacial thermal maximum, for under these conditions, as at Chandler Lake, spruce is an indicator of warm conditions. The *Isoetes* maximum lends support to this probability. According to Hultén (1941), *Isoetes* is known only from the temperate southern part of Alaska at the present time. Present knowledge of plant distributions in Alaska, particularly of inconspicuous water plants, leaves much to be desired and the plant may grow much closer to Death Valley than the published records show, but presumably if it were at all common in the sub-arctic parts of the territory it would have shown up at such accessible and well-botanized places as Fairbanks and Wiseman.

Isoetes is not an ideal climatic indicator, for its aquatic habitat and its predilection for rather oligotrophic lake bottoms introduce powerful non-climatic factors into its biogeography. Its absence from a particular lake at a particular time may mean nothing, but its presence must mean that the temperature was adequate to support it. At the time of the spruce maximum, this condition was fulfilled at Death Valley. At the present time, it is not known to be fulfilled north of the Alaskan Panhandle, 800 km. (500 miles) to the south.

Although the contemporaneity of the birch-alder transitions in the Chandler and Bettles regions is a matter of very great doubt, their vegetational equivalence is reasonably certain. This is a finding of some phytogeographic importance, because it implies that in this part of the interior basin of Alaska there was a time when conditions were as severe as they are at the present time far north on the Arctic Coastal Plain. The interior of Alaska has been regarded as an important refuge during glacial times and it must have been for many plants, but it would be unwise, in the face of evidence of such a marked vegetational change, to invoke it as a place of refuge for all the species which grow there today.

The incidence of fern and *Lycopodium* spores shows wide variation without any corresponding changes in the relative proportions of birch and alder. It would be possible to construct hypotheses concerning early snow cover to explain these changes, but their significance is not really understood. The majority of the spores are crushed, or have lost the outer layers of their exosporia, so that specific identification is impossible, but those which can be identified are all species which live in the interior of Alaska at the present day, and there does not seem to be any consistent change in their proportions from top to bottom of the core. It is quite possible that these changes may reflect only very local changes in the abundance of pteridophytes on the lake shore and have no regional significance.

DISCUSSION

It is impossible to see evidence, in the pollen profiles, of the general warming of the arctic which has been taking place during the past few centuries and particularly during the past 50 years. Pollen analysis of this refinement is not likely to reveal such a climatic fluctuation except under the most favorable conditions. As the results of this investigation show, conditions in tundra regions are not favorable for the registration of even such major climatic phenomena as the post-glacial thermal maximum. It is hardly to be expected that the much smaller recent warming could be detected by palynologic techniques.

The most striking thing about all these diagrams is the slightness of the vegetational changes which they reflect by comparison with pollen profiles from temperate latitudes. The greatest changes in a single profile, those of the Chandler Lake core, correspond to vegetational belts which can be found within a latitudinal distance of 500 km. (300 miles). Diagrams from northern Maine (Deevey 1951), which seem to cover a roughly comparable stretch of time, contain evidence of vegetational changes which cannot be reproduced today through a latitudinal distance of less than 2200 km. (1,400 miles). A likely deduction is that climate changes during the late Pleistocene have been much smaller, at least in terms of vegetational consequences, in this part of the arctic than in the temperate zone.

The north slope of Alaska forms a major part of the unglaciated Bering Sea region which has figured so largely as a refugium for the arctic and boreal flora in the theories of Hultén (1937). The possibility of survival through an Ice Age was established by the geologists who concluded that a large part of the arctic slope has escaped Pleistocene glaciation. The probability of survival was established by phytogeographic studies. The results of the present study indicate that a substantial fraction of the present flora was present during one of the minor late advances of the ice. The slightness of the vegetational changes that have taken place since the recession of this last glacier provides strong presumptive evidence that the region may have been an important refugium during full-glacial conditions as well. Further stratigraphic studies in the north slope would be necessary to provide conclusive proof of this.

The Brooks Range pollen record is free of the dramatic rises in the pollen of various shrubs which Iversen has found in Greenland, and which he has interpreted as evidence of immigration. This is not very surprising. With the exception of a few nunataks, none of south Greenland has escaped glacation. There was no large ice-free area near by into which *Alnus, Betula* and other shrubs could retreat and from which they could repopulate deglaciated Greenland. The unglaciated interior of Alaska, however, provides a refugium from which shrubs could repopulate the Brooks Range and the north slope of Alaska after each glaciation.

It is very interesting to speculate about the climatic significance of the apparent postglacial uniformity of northern Alaskan vegetation but the results should be checked elsewhere in the arctic, particularly in unglaciated Siberia and Greenland. Much longer stratigraphic sections and more detailed pollen analysis supported by macrofossil identifications would be required before one could reach reliable conclusions about climatic history.

Such evidence as is available from other places does not seem to contradict the findings of the present study. Apart from the shrubs, which appear to have been obliterated from southern Greenland by the physical presence of ice, Iversen (1950) did not find evidence of very spectacular vegetational and climatic changes in his cores from Godthaabsfiord. Indeed, the lowest levels of his cores contained the pollen or various thermophilous species from which he concluded that the temperatures at the time of ice retreat were not markedly different from present ones.

It is very difficult to know what significance to attach to the findings of Wenner (1944) in Labrador. Most of his diagrams cannot be interpreted because of the peculiar method which he adopted in calculating and graphing his pollen percentages. It appears, however, that in Labrador the vegetational changes since deglaciation have been intermediate in intensity between those of arctic Alaska and strictly temperate regions. One hopes that the renewed interest in the Pleistocene stratigraphy of the Québec-Labrador peninsula which has been manifest in recent years will soon lead to an understanding of the vegetational and climatic history of the forest-tundra border in eastern Canada.

Aario (1944), working with material from northern Lapland, has found rather great postglacial climatic changes. Although the sequence is somewhat less complex than that in temperate Europe, it is a good deal more so than the Alaskan one. This is only another aspect of the fact that patterns of oceanic circulation maintain temperate conditions at arctic latitudes in Fennoscandia.

If a general uniformity of Pleistocene climate in the Arctic could be demonstrated, it would be of the greatest interest, not only from the point of view of ecological history and general geography, but also because it would provide a datum of importance to paleoclimatology. The scarcity and imprecision of available paleoclimatic data have long delayed understanding of the Pleistocene epoch, for it is to climate change that this epoch owes its peculiar nature. In the absence of information speculation runs unchecked, as witness the host of rival theories to explain the phenomenon of glaciation.

It must be admitted that this study provides only a suggestion where a definite statement is needed. To argue from pollen through vegetation to climate is always a dangerous procedure. In this case, it may be particularly so. Very little is known about the meterologic valence of the various types of Alaskan tundra. It is possible that the changes from purely herbaceous tundra to tundra with birch shrubs and scattered alder bushes is of unexpected climatic significance even though it occurs in a short latitudinal distance. Neither the distribution of the tundra communities nor the weather of northern Alaska is known well enough for the accurate equation of the two.

In addition, there is a possibility that the whole record is much shorter than it appears to be—that it dates perhaps from the end of Boreal time or later. Although there have been great post-Boreal changes in the vegetation of temperate latitudes, it is by no means certain that these have been the result of simple climatic causes. They may have been due in part to phenomena of succession and migration which happen to have been absent from northern Alaska. In that case, the difference between arctic and temperate postglacial vegetational development would not be nearly so important as it appears.

Summary

A three-zone pollen chronology has been established for the region surrounding the central Brooks Range in northern Alaska.

The oldest of these zones, characterized by herbaceous tundra vegetation, appears to be contemporary with the Eschooka glaciation.

The youngest of these zones, characterized on the north side of the Brooks Range by tundra with shrubs and on the south side by hemiarctic vegetation, appears to include a weakly developed postglacial thermal maximum.

The longest core contains, in its herbaceous

zone, evidence of a temporary climatic deterioration similar to Zone III of the European pollen chronology. The sediments in which the evidence occurs are laminated.

The NAP/AP ratio of surface samples from a number of tundra lakes is much lower than the 1:1 that is usually taken to represent the division between forest and tundra.

About 50 different pollen and spore types were identified in the material. The principal pollen types were *Betula, Alnus, Picea, Salix* and Cyperaceae.

Vegetational changes during the time represented by the samples studied appear to have been much less striking than those of the temperate zone during the same time. This supports the view that the arctic unglaciated areas have served as glacial-age refugia for very many of the plants living in them today.

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MORTALITY OF OYSTERS AND ABUNDANCE OF CERTAIN ASSOCIATES AS RELATED TO SALINITY[1]

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INTRODUCTION

Dean (1892) saw that South Carolina oysters did not live below low tide in high-salinity areas and he postulated a previous "ostreous golden age" when there was more fresh water draining into the bays. Oemler (1894) noted failure of oyster plantings in high-salinity waters of Georgia and concluded that the American oyster could not endure waters of great density in the South. Ritter (1896) observed that oysters in Mississippi and Alabama did not "thrive so well" in waters of high salinity. Grave (1905) noted a much lower mortality following plantings in low salinity compared to those at high salinity in North Carolina waters. He said that reduction of salinity by a few points would exclude many oyster enemies. Pearse and Wharton (1938) found that attacks by the Florida oyster "leech," a turbellarian, declined during low-salinity periods. Various oyster growers and State officials have remarked, during the past fifty years, that oyster production bordering the lower Mississippi River failed as levees cut off fresh water and caused the salinity to increase (Gunter 1952). Ray, Mackin, and Boswell (1953) have stated that mortality caused by the fungus parasite *Dermocystidium marinum* is greatest in summer at moderate and high salinities in Louisiana. Some cases of high mortality associated with high salinity were mentioned by Sewell H. Hopkins in "History of some oyster mortalities reported in foreign countries," an unpublished paper read before the Symposium on Oyster Pathology held at Pensacola, Florida on February 1, 1950.

This communication presents certain data on the relation of oyster mortality to salinity. They were gathered in the course of a field study on the south Texas coast.

METHOD AND COLLECTION OF DATA

Two Sea Rac baskets were set up at each of five stations extending from Copano Bay to Aransas Pass, over a rising salinity gradient for a distance of 25 nautical miles. They were filled with oysters (*Crassostrea virginica*) tonged from nearby reefs and ranging from 1½ to 5 inches in length. Each basket was covered with another placed upside down and wired on. The top basket was covered with quarter-inch hardware cloth. Both baskets had two pieces of creosoted 6 x 8 inch timbers bolted lengthwise along the bottom. These served as a support above the sand and mud. The baskets were placed on the bottom and were raised for examination by a bridle of chain attached to each end. The depths were four to six feet.

Salinities and temperatures were taken once a week and the oysters were examined once a month. Dead oysters were counted and removed. The stations were numbered I to V in order of increasing salinity. The work was started in June 1949, but was not all set up until July and the period of the study may be said to be from July 1949 to January 1950.

OBSERVATIONS AND DATA

Salinity and Temperature

Table I gives the average monthly temperatures at all stations. From June to the middle of September the average water temperatures at all stations were very close to 30° C. They fell to a little below 25° at the last of September, but rose again to almost 28° on October 21. A 10° fall at the end of October was followed by a slight rise so that temperatures above 20° C. held during the last half of November and first half of December. The first "normal" winter temperatures were encountered on December 16, when the temperatures at all stations averaged 12.4° C. However, this low was followed by another rise, so that on January 16, the average temperature of all stations was 21.1°, and the highest reading was 22.0° C. The writer has shown (Gunter 1945) that the highest water temperature found in Copano Bay in January 1942 was 17.5° C. and the average was 14.9. Throughout the fall and winter months of 1949 and January, 1950, the newspapers published records of various days that broke long-standing or all-time high temperature records at Corpus Christi, Texas, twenty-five miles away.

There is no doubt that the winter of 1949-50, through January, was very warm on the Texas coast. This condition was reflected in the gen-

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[1] The data presented here were collected as a part of project 9 of the Texas A. & M. Research Foundation. The writer will always be grateful for the friendly cooperation of the late Dr. A. A. Jakkula, Director of the Foundation. He is similarly indebted to Dr. Sewell H. Hopkins and to Mr. E. H. Powell, Jr. for assistance in the field.

Table I. *Average temperature readings at all stations for the various months in °C*

Station	1949							1950
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
I.	30.9	30.4	29.2	28.1	23.5	19.8	15.8	15.7
II.	30.5	30.7	29.4	28.1	25.2	19.0	16.1	16.1
III.	29.5	30.7	29.7	28.3	24.9	20.3	16.0	16.3
IV.	29.0	30.5	30.3	28.7	25.6	20.4	15.3	16.5
V.	28.5	29.4	30.0	28.3	25.6	19.5	15.8	17.2
Number Readings	1	4	4	5	4	4	5	2

eral poor condition of market oysters in this region. They began to fatten a little in late October and early November. Then, as the oystermen put it, they "went backwards" and were very poor in quality in January.

Table II gives the average salinities at the stations for the various months. During the whole period of this work the salinities averaged higher in the bays than is ordinarily the case, especially in Copano Bay. From June 1941 to January 1942 the average salinity in Copano Bay was 7.9 (Gunter 1945). During the same time the average salinity of Aransas Bay was 19.9. From June 1949 to January 1950 the average salinities for the two bays, as determined by this study, were 19.6 and 26.4, respectively. During this time the salinities of Copano Bay were quite stable and some readings made near the Aransas River mouth showed that the salinity was practically uniform over the whole bay. The weekly salinity readings showed several times that the stations in Copano Bay and Copano Strait were saltier than the upper one in Aransas Bay, verifying the conclusion of Collier and Hedgpeth (1950) that the chief drainage of Aransas Bay comes from the Guadalupe River to the north rather than through Copano Bay.

In summary, during the time of this study both temperatures and salinities of Copano and Aransas Bays averaged higher than normal.

Table II. *Average salinities at all stations for the various months in parts per thousand. The number of readings were the same as for temperature*

Station	1949							1950
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
I.	17.1	17.4	18.3	20.8	21.1	19.8	18.8	18.6
II.	18.2	19.1	19.3	22.9	21.3	19.9	18.9	19.1
III.	24.0	22.4	23.3	25.9	21.3	21.6	18.7	19.6
IV.	27.6	27.8	29.1	29.7	22.7	24.5	21.3	21.8
V.	35.2	35.4	36.1	35.1	28.1	29.6	28.8	23.1

General Oyster Conditions

Oysters tonged from nearby reefs were placed at the various stations, so that they were not subjected to a different set of associates or different salinities and temperatures. Throughout the whole period the oysters were in relatively poor condition, so far as their market qualities went. Oysters at station III were better than at any other station.

The condition of oysters is generally correlated with temperatures on the Gulf Coast and oysters only become fat in the fall and winter after temperatures drop. The writer (Gunter 1942) has previously presented evidence on this subject. Since temperatures were abnormally high, there is no puzzle about the poor condition of the oysters during the fall and winter of 1949-50. The importance of this situation in regard to the present investigation is that mortality was probably higher during the cold season than in other years. Therefore, the differential seasonal mortality between summer and winter was probably not as much as in more normal years.

The abnormal season was also reflected in the abundance of spat or small oysters throughout the fall and winter. Oyster spat, noted on the sample oysters at the time they were placed in the baskets, attained such size in a few months that there was likelihood of confusing them with the test oysters. Therefore, on October 13 all oysters were reculled and the spat removed. At this time spat was most abundant at station III and next most abundant at station IV. However, at station IV approximately half of the spat was found to be *Ostrea equestris*. Although the salinities of III and IV were not greatly different and the distance was only a matter of a couple of miles, only one *O. equestris* was noted at station III. In spite of the removal of all spat in October, when the work was stopped in January the test oysters were again abundantly sprinkled with little oysters from spat size to almost one-half inch long. Again they were most abundant at station III and least abundant at V and I. As stated previously, the water temperatures in January were often above 20° C., and spawning evidently took place in the late fall or winter.

Growth measurements were not made. However, sharp-edged, new shell was more noticeable on October 6 than at any other time and the oysters at station III showed the greatest amount.

Oyster Mortality

The general conditions of currents, wind and waves were much the same at all stations except at number V under the laboratory dock at Port

Aransas. Here the baskets were wired solidly to cross timbers of the dock, because experience had shown that Sea Rac baskets on the bottom were overturned by wave wash from boats or from surf entering the pass. Both *Thais haemostoma,* the oyster borer, and *Menippe mercenaria,* the stone crab, entered the baskets and caused heavy mortality. Stone crabs are very strong. They tried to go through the metal hardware cloth by squeezing the mesh together, and evidently they squeezed between the two baskets where they were wired together. However, larger crabs were found in the baskets than could come through any visible entrance and it was assumed that they grew after entering the baskets. After the oyster was eaten, stone crabs continued to crack the shell into smaller pieces for the purpose of getting the worms and boring clams, *Martesia,* in the shell. These small pieces washed through the mesh of the baskets. A large bucket of cracked shell was recovered. In July and August, 400 of the original 432 oysters disappeared from the baskets at station V. Therefore, the per cent of natural mortality for July and August at this station was deduced from losses rather than from the number of dead shells or boxes. Mortality caused at this station by *Thais* and *Menippe* was excessive and far exceeded that at any other station. In September more oysters were added to one basket, which was then suspended, swinging free in the water and covered tightly with hardware cloth. From that time on complete boxes of dead oysters were recovered and no more were lost.

Fifty-one oysters were removed from the baskets for parasitological examination. At various times some oysters were replaced at various stations. Some oysters were lost from the baskets and a considerable number were killed by mud when baskets were overturned as the result of high winds. One basket was torn from its lashings and lost completely. These events occurred in such a way that a uniform table describing the history of each station is rather difficult to make and would be confusing. Therefore, the results are presented by the numbers of survivors and natural mortality, in cases where actual boxes of the dead oysters were recovered. Table III shows the number of oysters placed at each station, those dying from biological causes, and the percentage of mortality. The mortality at station V is presented in two sections. That up to September was considered to be predator mortality and is listed first. The non-predatory mortality from October to January, is listed second. At the other stations mortality for the whole period was utilized. At station V, although the time was two months shorter, the second mortality was approximately 50 per cent, or roughly five times as high as that at the low salinity stations. None of this later mortality at station V was caused by the stone crab or *Thais.* At the four inner stations the mortality was approximately 10 per cent and was not significantly different at any of them.

TABLE III. *The number of oysters placed at each station, the number and the per cent that died are shown. The figures cover the period from July 1949 to January 1950, except for station V, as stated in the text*

		Alive	Died	
			Number	Per Cent
I		419	48	11.5
II		589	64	10.9
III		554	45	8.1
IV		475	52	11.0
V	J-A	432	390	90.3
	S-J	161	80	49.7
Totals		2,640	678	25.7

Table IV shows the natural mortality at each station each month and the percentage mortality for all stations combined for each month. It was much higher during the summer, although the high fall and winter temperatures, already commented upon, would tend to minimize seasonal differences of mortality.

TABLE IV. *The number of oysters dead from natural mortality at each station each month and the average monthly percentage mortality for all stations combined. The first two months are combined and the figures are totals for that period. The number of live oysters placed at each station are shown in Table III. For further explanation, see text*

Station	July-Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
I	4	3	4	19	9	9
II	5	24	5	6	12	12
III	28	8	3	..	5	1
IV	13	12	17	6	4	..
V	390	9	45	9	13	4
Totals	440	56	74	40	43	26
Per Cent	17.8	2.8	3.6	2.1	2.5	1.7

Except for the initial high predator mortality at station V, the average mortality at all stations (circa 2.5 per cent per month) is relatively low, and evidently oysters kept in large, tarred, metal baskets (Sea Rac), and thus partially protected from their enemies, live very well. This mortality is considerably less than that on natural reefs or planted oyster beds, as the most elementary calculations of normal annual yields of planted oysters will show.[2] Hewatt and Andrews (1954) came to the same conclusion by similar reasoning, saying (p. 131) "There are reasons to believe that natural mortalities exceed those encountered in trays. . . . This belief is not based on a measurement of natural mortalities but on analysis of yields." Thus, oyster mortality in baskets resembles natural reef mortalities only in a very general way and the data are not to be taken as precise measurements of mortality or survival on natural beds.

General Faunal Characteristics

The chief changes or outstanding biological characteristics at each station were fairly simple and can be noted briefly. In August the presence of *Menippe*, the stone crab, was evident at all stations. Their depredations were noted until November. The oyster borer *Thais* was present only at station V. It attacked oysters until October. Afterwards none were seen. In August considerable yellow boring sponge, *Clione* sp., was noted on the oysters at stations I, II and III. Thousands of the small flat crab *Petrolisthes armatus* were present at station III. At station IV patches of red sponge, *Microciona prolifera*, occurred. *Petrolisthes* also became very abundant at Station IV in September and thousands of these little crabs remained at stations III and IV until October. The red sponge became abundant at stations II and III and very abundant at IV in September. It declined slowly until none was left in winter. During its greatest abundance this sponge covered the oysters, the baskets and the attached algae almost completely at station IV, so that the whole ensemble had the appearance of having been dipped in carmine paint. During December and January prolific colonies of the hydroid *Tubularia* grew on the basket at Port Aransas. Many ctenophores and the jellyfish *Aurellia aurita* were present at the bay stations during the warm months. The latter species greatly outnumbered *Dactyolometra quinquecirrha*, which is usually the most common bay jellyfish.

By and large animal life became least abundant in the winter, except for *Tubularia*, as noted above. Large numbers of calcareous worm tubes were noted on the oysters and baskets at Station I in November. The bryozoan *Acanthodesia* was extremely thick at station IV in October, its encrustations covering the oysters, the baskets and the alga *Acetabularia*.

DISCUSSION

In the area studied the salinity of the upper and back bays was rising, due to a long drought, and was becoming more equivalent to that of the lower bays. The oyster borer *Thais* was not present at any station except V, although the salinities were well within its range of tolerance at all stations during the period studied. It seems that neither the adult animal nor its larvae could cover the distance from Port Aransas to Rockport or Copano Bay, the minimum distance being eleven miles, during this eight-month period.

The salinities at stations I, II and III were almost uniform from October to January and yet the general animal communities did not come into equivalence and, similarly, spatfall and fatness of the oyster were quite different between stations I and III. Station III oysters were quite heavily coated with red sponge but this sponge never became abundant at station I. The small crab *Petrolisthes* was present in the thousands at station III, but much less abundant at station II, which was very comparable in terms of temperature and salinity, the average salinity difference being 3.6 per mille. On the other hand this little crab was extremely abundant at station IV where the salinity was only 3.7 per mille higher than at station III. The difference of spatfall of *Ostrea equestris* at these two nearby stations has already been mentioned. In December vast numbers of unidentified calcareous worm tubes were found on the oysters in the baskets at station I. They were not very abundant at station II, although the physical conditions at II were very similar. Obviously, although salinity is a very important environmental characteristic, marine biotic communities exhibit a strong inertia when subjected to salinity change and do not become equivalent in areas of equivalent salinities for a long time. On the other hand, the small salinity differences, 3 to 4 parts per thousand, may exert more differential influence than is realized or expected.

The causes of oyster mortality are usually impossible to ascertain when only the empty boxes remain. One significant thing noted was that nearly all boxes showed a high incidence of mudworm blisters or penetration by the boring sponge or both. Smith (1935) made similar observations concerning an oyster mortality in Louisiana in 1934. It is not believed that these animals are directly responsible for oyster mortality, except possibly in rare instances, but rather that they were contributing factors by opening the way for other invaders. Very few boxes showed penetration by the boring clam. The cracked shells found at station V indicate that the heavy initial mortality there was caused by the stone crab, most likely with the assistance of *Thais*, which, however, may leave no mark. The fungus parasite *Dermocystidium* has never been found in the area studied and apparently it does not exist on this part of the Texas coast. Nevertheless, nonpredator mortality in this study corresponded to *Dermocystidium* mortality reported from other areas in being highest in high salinity (cf. Ray, Mackin, and Boswell 1953).

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[2] It is remarkable that more extensive studies of the practical question of "normal" mortality on oyster beds have not been made. References in the literature to mortality studies are generally concerned with catastrophes. Commercial oystermen on the Gulf coast commonly get a one-to-one volume yield of adult oysters from seed planted the year before. The differences in size of the two groups make up for an annual mortality which may approach 90 per cent, depending upon the initial size of the seed. Owen (1953, p. 48) has prepared a table showing that in growing from 45 to 85 mm. in length, oysters will maintain a 1:1 volume yield at a mortality of 85.1 per cent. Oyster biologists commonly consider evidences of a four- or five-per cent recent mortality on beds as normal.

The numbers of species of marine animals decline along the salinity gradient going toward fresh water (Gunter 1945, 1950). Thus, as Grave (1905) has previously noted, oysters are subjected to greater predation and parasitism at higher salinities. Apparently, that situation explains the higher incidence of predatory and nonpredatory mortality in higher salinities, as observed in this and other studies.

Summary

A field-mortality experiment on oysters was carried on from July to January 1949-50, inclusive, in Copano and Aransas bays on the south Texas coast. Salinities were higher than usual during this period and water temperatures during the fall and winter were much higher than normal.

At four stations the salinities were low and not greatly different and the mortality was not significantly different. Predator mortality was high at the high-salinity station during the summer. This led to a considerably higher summer mortality, as compared to fall and winter, when all stations are taken together. At a high-salinity station mortality not due to predation was approximately 50 per cent from September to January. At the other four stations the mortalities from June to January were close to 10 per cent. Both predator and non-predator mortality was greatest in oysters at high salinity. The great majority of oyster boxes showed a high incidence of mudworm blisters and boring sponge penetration.

Mortality of oysters partly shielded from enemies in Sea Rac baskets is low. Oysters showing the most shell growth were in the best condition and showed the greatest abundance of spat at a station near the best oyster reefs in Aransas Bay. During the time of the study this location did not vary greatly in temperature or salinity from stations on either side of it. Similarly, at adjacent stations where salinities differed by only 3-4 parts per thousand, and were practically uniform for months at a time, the incidence and abundance of the oyster associates *Petrolisthes*, serpulid worms, red sponges, bryozoa and others, did not become the same but remained clearly different.

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PHYTOSOCIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF SOME PLANT COMMUNITIES IN THE UMIAT REGION OF ALASKA[1]

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Introduction

The purposes of this investigation were to determine some of the kinds of plant communities which make up the vegetation in the Umiat area of Alaska, to analyze the communities phytosociologically, to study some of the relationships of such communities to environmental conditions, and to obtain information for aerial photographic interpretation.

Umiat is located at 69° 22′ N, 152° 08′ W. The elevation on the floodplain at Umiat is approximately 340 feet as reported by the U. S. Weather Bureau (1952a). Elevations of the ridges and tops of hills of the upland extend to 950 feet.

Very little is known of the various kinds of plant communities of the Umiat area, especially regarding cover and frequency of constituent species, interrelations of communities, and environmental relationships. Lepage (1949), Retallick (1950), and Spetzman (1951) described briefly some broad vegetation types. Sufficient knowledge of the communities would probably permit the use of such communities as indicators of environmental conditions. Because of the complexity of communities of this area, detailed qualitative and quantitative data are required to understand the interrelationships of the communities. They are also needed as a basis for developing a reliable aerial photographic interpretation technique.

Data on the floristic composition, cover, frequency and environment were collected for 80 stands during July and August, 1951. Quantitative data had never been obtained in this area and the amount of such data on plant communities in Alaska is very limited, therefore no attempt was made to establish successional trends or to devise a classification system similar to those in use in Scandinavian and other European countries.

On the basis of phytosociologic analysis of association tables and indices, the stands are grouped into 5 types, 1 of which is divided into 4 subtypes and another into 2 subtypes. Selected stands of each type and subtype are discussed in detail, association tables of some of these stands and of each subtype and type are included and each subtype and type is discussed as such.

Procedures and Methods

Field procedures

The field work was performed during July and August, 1951. Herbarium specimens were collected and those of vascular plants have been deposited in the Langlois Herbarium of The Catholic University of America.

The stand was used as the unit of study. The tundra vegetation of the Umiat area displays in many cases variation within a few feet or inches, probably as a result of the variation in environmental conditions accompanying a few inches difference in microrelief and resulting in a micromosaic of microstands. Each stand has a homogeneity of micromosaics that is distinctive over a given area and is dissimilar to the distinctive homogeneities of adjacent areas. The stands are numbered in the order of analysis in the field.

The selection of stands for analysis was based on the study of all available aerial photographs of the area and on ground reconnaissance, that is, by homogeneity of appearance of each stand both on aerial photographs and on the ground. Analysis was also made of stands which were perceptibly different on aerial photographs yet appeared similar on the ground, and those which were nearly identical on aerial photographs yet dissimilar on the ground. Frequently adjacent communities,

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[1] A dissertation submitted to the faculty of the Graduate School of Arts and Sciences of the Catholic University of America in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] The writer wishes to acknowledge his gratitude to Dr. Herbert C. Hanson for his guidance in this problem and assistance in preparation of the manuscript and to Dr. Hugh T. O'Neill and Dr. John A. O'Brien for very helpful criticism and assistance. Appreciation is also expressed to the following:

The U. S. Air Force which made possible temporary duty at Umiat, Alaska during the summer of 1951.

The U. S. Navy for permission to conduct field investigations in the Umiat area.

Members of the staff of the Boston University Physical Sciences Research Laboratory, especially Dr. Franklin C. Erickson, Charles Matthews, Ralph Fellows, and James Maxwell, who assisted in the collection of field data and for ground photographs.

Rev. Ernest Lepage, O.M.I., for identification of vascular plants, Dr. Jason R. Swallen for identification of grasses, Dr. Carlton A. Ball for identification of willows, Dr. Howard A. Crum for identification of mosses, and Dr. A. Leroy Andrews for identification of Sphagna.

Dr. Constantin C. Nikiforoff and Arnold C. Orvedahl of the Division of Soil Survey, U. S. Department of Agriculture, for advice on the collection of soil data.

especially of the upland, were very similar and the zones of transition from one to another were so gradual and over a sufficiently great distance that detection by only ground reconnaissance would have been very difficult and time consuming. With respect to similarity and zones of transition the communities resembled the continuum described by Curtis and McIntosh (1951). In several cases, significant differences between adjacent communities were readily detected on aerial photographs although the differences were not readily detected by ground reconnaissance. At times, only after comparison of detailed sample analysis data were the differences detected; post-sampling ground reconnaissance confirmed the differences.

The vegetation of each stand was analyzed on 10 one-meter square quadrats which were systematically located as uniformly and widely as possible but restricted so that transitional areas into adjacent stands were avoided. The cover of each species of vascular plants, grouped mosses, grouped lichens, and area of bare ground was estimated by a modified Hult-Sernander scale (Nordhagen 1943, Hanson 1953), as follows:

Cover class	Cover
1	to 1/16
2	1/16 to ⅛
3	⅛ to ¼
4	¼ to ½
5	½ to ¾
6	¾ to 4/4

The Hult-Sermander and similar cover scales have been used extensively in Scandinavia and other parts of Europe (Braun-Blanquet 1932, Dahl 1953a). Objections have been made to cover class 5 of the Hult-Sernander scale, which is from ½ to ¾ of the area, as being too large. For that reason the cover class 5 was divided into classes 5 and 6 in the modified scale. Analysis by the modified Hult-Sernander scale was adequate to sample the cover and the homogeneity of micromosaics within each stand and was particularly appropriate for both phytosociological analysis and aerial photographic interpretation purposes.

A cover-frequency reconnaissance method was tried on an experimental basis at the close of the field season. In the reconnaissance method, the cover is estimated directly for the whole stand and the frequency of each species is estimated on a scale of 10 classes so that such estimates can be compared directly with detailed analysis date of other stands. The reconnaissance method, if further developed, should have considerable merit because it yields comparable data to that obtained by detailed cover analyses on 10 one-meter square quadrats. The reconnaissance method can be readily checked for accuracy by making detailed analysis on 10 one-meter square quadrats within the stand in question.

A soil profile of each stand was described by layers without naming or identifying the horizons since so few profiles had been previously described and analyzed in the arctic. Little is known concerning the morphology and there has been little development of nomenclature of tundra soils. A special terminology may be needed for tundra soils (Nikiforoff 1951).

Analysis of data

The floristic-characteristic-species-combination (Raabe 1950) consists of those species of a community with the highest frequency, the number of such species being equal to the average number of species per sample area, per square meter in this investigation. Determination of this floristic-characteristic-species-combination for each stand and a preliminary grouping of stands on the basis of this combination were of assistance in the preliminary analysis of data. The Central European ecologists have found that the kind and number of species which make up this combination are distinctive and that this combination characterizes the community (Raabe 1950). Additional data on the communities of the Umiat area would be required to determine whether the floristic-characteristic-species-combination could be one criterion for a classification of the communities.

There are numerous coefficients which can be computed to determine the degree of relationship between two communities. The coefficient of affinity, based on the average difference of frequency in common of all species in the two stands being compared (Sörenson 1948) was also computed. According to Dahl (1953b), the Sörenson coefficient is more sensitive and analysis of the Umiat data tended to confirm this.

Raabe (1952) described a homogeneity value which is the average frequency value of the floristic - characteristic - species - combination; the higher this value, the more homogeneous the community. This homogeneity-index is given for each stand in each type and subtype association table. Dahl (1953a) described a homogeneity test which is readily computed in the field. If the number of all species with a frequency of 81 to 100%, class V, is greater than the number of species with a frequency of 61 to 80%, class IV, then the community is considered to be homogeneous. At times even though this test is negative for homogeneity it may be desirable to use the analysis of the stand; for example, in aerial photographic interpretation. This frequency-homogeneity test is also given for each stand in the type and subtype association tables. Either or both homogeneity tests aid in the analysis of data and are of value as indices for the analysis of homogeneity of registration of stands on aerial photographs.

While these procedures were useful in analyzing data and grouping stands, final analysis and grouping were dependent primarily upon thorough study of the association tables.

Environmental Data

Geology

The Umiat area is within the Northern Foothills section of the Arctic Foothills province on the slope north of the Brooks Range. Due to relatively simple structure there is a great regularity of topography, with ridges, mesas, and hills that are of very similar altitude (Payne, *et al.* 1951). The general topography of the upland is gently rolling hills and moderately flat valleys (Smith and Mertie 1930). Polygonal ground occurs on poorly drained areas (Black and Barksdale 1948).

The Umiat area was divided by Black and Barksdale (1948) into the bedrock hills or upland and the floodplain of the Colville River; the latter was divided into the high terrace and the low terrace. The high terrace is from 6 to 8 feet above the low terrace and is characterized by poor drainage, numerous lakes and ponds and well-developed polygonal ground. The low terrace is generally less than 10 feet above the Colville River and is characterized by the presence of abandoned channels, oxbow lakes, and poorly developed polygonal ground. Black and Barksdale stated that: "The floodplain deposits of the Colville River in the Umiat area consist of lenticular bars of silt, sand and gravel formed along active channels, and muck and silt deposits in abandoned drainage channels." They also pointed out that the low terrace is subject to flooding during the spring break up.

The upland plant communities studied were located on the Umiat anticline which has predominantly low dips on both flanks and is modified near its axis by a monoclinal flexure approximately parallel to the crest of the anticline (Stefansson and Whittington 1947). The rocks in this area are of Upper Cretaceous age. The description of the upper 1,100 feet of the formations of this anticline by Stefansson and Whittington covers the area of study. The sequence consists predominantly of silt shale and clay shale with numerous interbeds of sandstones, some of which are highly calcareous. There are some interbeds of pyroclastics (bentonite and tuff) present.

Climate

The climate of the Umiat area is rigorous. The average annual temperature is 10.7°F; the lowest recorded temperature was —63° during February, the highest 85° during July, and the mean monthly temperature is below 0° for the period December through April. The averages are for the period April 1, 1945, through October 31, 1952, 7 years for November through March and 8 years for April through October (U. S. Weather Bureau 1952a, 1952b).

The average monthly temperature has been above 32.0° only during the period June through September. The data concerning the mean number of days per month when the maximum temperature has been equal to or greater than 70° and equal to or less than 32°, and the mean number of days when the minimum temperature has been equal to or less than 32°, have greater significance than the averages. These data on means indicate that in April only 2 days can be expected with a maximum temperature above 32° and in May, 10 days. Freezing temperatures occurred each day in May. During the period June through August, the maximum temperature was not below 32° but freezing temperatures have been recorded on an average of 14 days during June, 2 during July, and 8 during August. During September, the average number of days with a maximum temperature above 32° was 22, minimum temperatures of 32° or less occurred on 24 days, and 0° or less on 1 day, and during October the average number of days with a maximum temperature above 32° was 3. Since a freeze-free season cannot be expected, the species of plants which occur in the area must have a high tolerance to cold. It may be assumed that vegetative growth on the average could begin in May and continue through part of August, possibly extending into September to a very small degree.

Long-enduring subfreezing temperatures of great intensity during most of the year and relatively low average summer temperatures account for the frozen ground at depths of 6 to 18 inches even at the time of maximum ground thaw. On gravelly and sandy soils, frozen ground is encountered at greater depths. The temperature gradients in mineral soil from the surface to the frozen soil are very steep and even though sufficient moisture is present for plants, the absorption rate, except in the uppermost portion, must be low. The presence of frost scars and polygonal ground is visual evidence associated with the intensity and frequency of freezing.

Regardless of the low annual precipitation, 5.79 inches, the climate is not arid with respect to plants since the temperatures and evaporation rate are low and relative humidity is high. The dense cover of vegetation, accumulation of organic matter, and microrelief tend to favor absorption and to retard runoff.

Little is known concerning the nature of snow cover during the winter. However, examination of a sortie of winter aerial photographs revealed a complete snow cover and examination of a sortie of early summer photography revealed some snow banks not yet melted, indicating drifting snow as a result of wind action during the winter. The degree of exposure to prevailing winds during the winter would thus determine the variable depth of snow and accompanying insulation effect on the various sites.

It was noted that the upper 6 to 9 inches of terminal portions of willows which had reached about 3 feet in height on the upland had been killed, probably as a result of either wind desiccation or the abrasive effect of wind-blown snow during the winter.

The direction and degree of slope are undoubtedly of great importance on the effect of exposure to winds during the winter, the accumulation of snow, the rate of snow melt due to the incidence of solar radiation, the rate of surface runoff, and the amount of solar radiation received and available for ground thaw and for growth of plants during the summer.

Discussion of Communities

On the basis of floristic composition the stands are classified into 5 major groups as follows:

I. Dwarf Shrub Heath Type
II. Frost-Scar Collective Type
III. Salix Type
IV. *Alnus crispa* Type
V. *Carex aquatilis*—Marsh Type

Summary association tables are included for each type or subtype.

I. Dwarf shrub heath type

The dwarf shrub heath type is classified into subgroups according to differences in the frequency, cover, and in some cases the occurrence of certain species. In the first subtype (Table I), *Eriophorum spissum* is of outstanding importance; however, it is replaced by *Eriophorum vaginatum* in Stand 27. The nearly equal frequency of *Eriophorum spissum, Carex lugens,* and *Arctagrostis latifolia* in the second subtype is an important characteristic. The third subtype has as a prominent characteristic the presence of *Carex* spp. The relatively high frequency of *Arctagrostis latifolia* is the outstanding characteristic of the fourth subtype.

1. *Eriophorum Tussock-Dwarf Shrub Heath Subtype.*—Twenty-two stands are grouped in this subtype (Table I) on the basis of high or moderately high frequency of *Eriophorum* spp. and dwarf shrub heath species and associates, especially *Betula nana* ssp. *exilis, Empetrum nigrum, Ledum decumbens* and *Vaccinium vitis-idaea*. In the first 18, *Carex lugens* is associated with *Eriophorum spissum* and with *E. vaginatum* in Stand 27. The last 3 stands form a subgroup because of the replacement of *Carex lugens* by *C. consimilis* but with respect to *Eriophorum spissum* and dwarf shrub heath species they belong to this subtype. The Eriphorum Tussock-Dwarf Shrub Heath Subtype has a widespread distribution on the upland, slopes and floodplain. Representative stands are selected for detailed discussion.

Stand 20. *Alnus crispa-Eriophorum spissum*-dwarf shrub heath

This stand, located on the upland 1.5 miles north of Umiat, had a south exposure and was on a slope of 10°. Lateral microrelief, essentially on the contour, had a maximum of 14 inches and an average of 6 inches, while the microrelief of the slope had a maximum of 18 inches and an average of 10 inches. The microrelief resulted from the presence of mounds up to 4 feet in diameter which had abrupt down-slope faces and more rounded up-slope faces, the whole having the appearance of dissected small contour terraces. The presence, arrangement, and shape of the mounds were indicative of soil movement. Surface drainage was well-developed, the microchannels being from narrow with high gradient to broad with low gradient. The site was generally dry. Vegetation characteristics (Table I) of this stand are the high frequency of *Alnus crispa, Eriophorum spissum,* 5 dwarf shrub species, mosses and lichens.

Stand 70. *Salix pulchra-Eriophorum spissum-Carex lugens*-dwarf shrub heath

This stand, 0.8 mile northwest of Umiat, was located on the flood-plain, near the edge of the low terrace, adjacent to a meander scar. The site was level, exposed to winds from all directions and no development of surface drainage was apparent. The area was dry because of the gravel and sand constituents of the terrace. There was

TABLE I. *Frequency and cover of species in the Eriophorum Tussock-Dwarf Shrub Heath Subtype. Cover is given as an exponent of frequency*

Species	Stand 70	Stand 28	Stand 2	Stand 63	Stand 15	Stand 73	Stand 54	Stand 12	Stand 59	Stand 58	Stand 41	Stand 20	Stand 53	Stand 74	Stand 10	Stand 62	Stand 65	Stand 69	Stand 27	Stand 50	Stand 3	Stand 29
Eriophorum spissum Fern.	100^{2-}	100^{1+}	100^{1+}	100^{3-}	100^{1}	100^{2}	100^{1+}	100^{1+}	100^{1+}	100^{1+}	90^{1+}	90^{1}	100^{2}	70^{1}	100^{1+}	100^{4-}	100^{3+}	40^{1}		100^{1+}	100^{1+}	100^{1}
Eriophorum vaginatum L.																			70^{1}			
Eriophorum angustifolium Roth													10^{1}									
Carex lugens Holm	100^{2-}	90^{1}	70^{1}	70^{1+}	90^{1}	80^{1}	30^{1}	20^{1}	40^{1}	100^{1}	30^{1}	10^{1}	100^{1}	100^{2-}	100^{1}	20^{1}	+	50^{1}	100^{1}	+		
Carex capillaris L.										+				+								
Carex consimilis Holm									+											80^{1}	60^{1}	20^{1}
Carex rariflora (Wahl.) J. F. Smith														+								
Carex aquatilis Wahl.	+																					
Luzula confusa Lindeb.		10^{1}				40^{1}	+			30^{1}										10^{1}		
Luzula nivalis (Laest.) Beurl.				10^{1}				40^{1}	30^{1}		10^{1}											
Juncus albescens (Lge.) Fern.																				10^{1}		
Juncus castaneus J. E. Smith																				10^{1}		
Arctagrostis latifolia (R. Br.) Grieseb.	10^{1}	10^{1}			10^{1}	40^{1}	+	20^{1}	20^{1}	20^{1}		10^{1}	+					10^{1}	20^{1}	10^{1}	10^{1}	10^{1}
Hierochloe alpina (Sw.) Roem. & Schult.	+								40^{1}		40^{1}	10^{1}								20^{1}		
Poa arctica R. Br.	20^{1}					10^{1}														10^{1}		
Ledum decumbens (Ait.) Lodd.	100^{1+}	100^{1}	100^{1}	100^{2-}	100^{1}	100^{1+}	100^{1}	100^{1}	100^{1+}	90^{1}	90^{1}	100^{1}	60^{1}	90^{1}	100^{1}	100^{1+}	100^{2+}	100^{2-}	100^{1+}	100^{1}	100^{1}	100^{2-}
Vaccinium vitis-idaea L.	100^{2-}	100^{1}	100^{1}	100^{2-}	100^{1}	100^{2-}	100^{1}	100^{1}	90^{1}	90^{1}	100^{1}	100^{1}	70^{1}	80^{1}	90^{1}	100^{1}	100^{3+}	100^{3}	100^{1}	100^{1}	100^{1}	100^{1+}
Vaccinium uliginosum L.	100^{2-}	20^{1}	50^{1}	30^{1}	40^{1}		30^{1}		20^{1}	40^{1}	80^{1+}	100^{1}	100^{1}	10^{1}	20^{1}				40^{1}	50^{1}	100^{1}	
Betula nana L. ssp. *exilis* (Sukatch.) Hult.	100^{1+}	100^{1}	90^{1}	90^{1+}	90^{1}	100^{1}	100^{1}	100^{1}	100^{1}	100^{1}	100^{1+}	90^{1+}	60^{1+}	70^{1}	100^{1}	20^{1}	100^{1+}	90^{1}	100^{1}	100^{1}	100^{1}	100^{1}
Arctostaphylos alpina (L.) Spreng.	10^{1}	80^{1}		60^{1}	80^{1}	80^{1}	10^{1}		20^{1}	10^{1}	50^{1}	100^{1}	70^{1}		30^{1}	10^{1}	10^{1}		70^{1}	80^{1}		80^{1}
Cassiope tetragona (L.) D. Don.		40^{1}	90^{1}	10^{1}	90^{1}	90^{1}	50^{1}	100^{1}	80^{1}	90^{1}	50^{1}	70^{1}	100^{1}		100^{1}	+				60^{1}	100^{1}	
Empetrum nigrum L.	100^{2-}	100^{1}	90^{1}	90^{1}	70^{1}	80^{1}	100^{1}	70^{1}	70^{1}	70^{1}	100^{1}	90^{1}	40^{1}	100^{1}		+	50^{1}	30^{1+}	70^{1}	90^{1}	90^{1}	90^{1}
Rubus chamaemorus L.	50^{1}	70^{1}				70^{1}		+				10^{1}		60^{1+}	20^{1}	90^{1}	90^{1+}	100^{3-}	10^{1}	+		
Andromeda polifolia L.		40^{1}									40^{1}			100^{1}	40^{1}	10^{1}			10^{1}		20^{1}	
Alnus crispa (Air.) Pursh.	10^{1}	30^{1}	10^{1}							+	40^{1}	80^{1+}							50^{1+}		80^{1+}	30^{1}
Salix glauca L.					10^{1}					+			+							+		
Salix pulchra Cham.	100^{1+}	50^{1}				10^{1}	80^{1}	90^{1}	60^{1}	90^{1}				20^{1}					30^{1}	50^{1}		
Salix phlebophylla Anderss.									30^{1}		10^{1}									60^{1}		
Salix niphoclada Rydb.										70^{1}			30^{1}						+			
Salix brachycarpa Nutt. var. Mexiae Ball.	20^{1}																					
Salix pulchra Cham. var. *Palmeri* Ball			80^{1}		100^{1}								70^{1}		90^{1}				+		30^{1}	
Salix reticulata L.										30^{1}			60^{1}									
Salix desertorum Rich.													+									
Salix pulchra Cham. var. *yukonensis* Schn.										+	50^{1}											10^{1}
Salix glauca L. var. *glabrescens* (Anderss.) Schn.			30^{2}																			

TABLE I—*Continued*

Species	Stand 70	Stand 28	Stand 2	Stand 63	Stand 15	Stand 73	Stand 54	Stand 12	Stand 59	Stand 58	Stand 41	Stand 20	Stand 53	Stand 74	Stand 10	Stand 62	Stand 65	Stand 69	Stand 27	Stand 50	Stand 3	Stand 29
Salix fuscescens Anderss. var. *reducta* Ball														70^1								
Salix rotundifolia Trautv.							20^1															
Spirea beauverdiana Schneid.											+											
Polygonum bistorta L. ssp. *plumosum* (Small.) Hult.		20^1	80^1	30^1	100^1	30^1	20^1	40^1	80^1	60^1	70^1	80^1	30^1						40^1	40^1	40^1	30^1
Pyrola grandiflora Radius	20^1		10^1							80^1			30^1		10^1							
Stellaria Laxmannii Fisch.							+		+	10^1									20^1	10^1		
Petasites frigidus (L.) Fries	30^1				20^1	40^1		60^1					10^1		20^1				10^1			
Pedicularis capitata Adams	40^1	30^1	10^1		10^1								20^1		50^1				10^1	50^1	10^1	
Pedicularis labradorica Panzer						30^1		30^1				10^1										
Pedicularis lanata Willd.				20^1			40^1	40^1	10^1	50^1	50^1					20^1						
Saussurea angustifolia (Willd.) D. C.	10^1				10^1			50^1		10^1			20^1									
Lupinus arcticus Wats.									10^1											10^1		
Senecio frigidus (Richards.) Hook.		10^1			+				+	20^1			+						10^1	+		
Antennaria isolepis Greene							+													+		
Saxifraga punctata L. ssp. *Nelsoniana* (D. Don.) Hult.			20^1		20^1	40^1	+	20^1	10^1	30^1										+		
Arnica lessingii Greene							40^1		+	10^1												
Rumex acetosa L. ssp. *alpestris* (Scop.) Love							10^1															
Pedicularis sudetica Willd.														20^1								
Lycopodium selago L. var. *appressum* Desv.																20^1						
Equisetum arvense L. var. *boreale* (Bong.) Ledeb. f. *pseudo-varium* Viet.										+												
Mosses	100^5+	100^5−	100^4+	100^4+	100^2+	100^5+	100^3+	100^3	100^6−	100^5	100^3+	100^2+	100^4+	100^6−	100^3−	100^5+	100^5	100^6−	100^3+	100^5+	100^3−	100^3+
Lichens	100^3−	100^2−	100^1+	100^3−	100^2	100^4+	100^1+	100^1+	100^2+	100^2−	100^2−	100^3−	100^1+	100^1	100^1	100^3+	100^3−	100^2+	100^2−	100^2+	100^1	100^3+
Bare ground								70^1+	10^1	10^1	50^1+											
Total vascular species in quadrats	18	18	15	13	16	17	15	17	18	23	16	16	19	13	14	9	7	8	18	21	14	11
Average number vascular species per quadrat	10	10	10	7	11	10	8	10	9	12	10	10	10	9	10	5	6	5	9	11	99	7
Homogeneity-index	89.0	83.0	85.0	87.1	87.3	84.0	83.8	81.0	80.0	82.5	78.0	90.0	79.0	83.3	85.6	82.0	90.0	88.0	77.8	79.1	92.2	85.7
Frequency-homogeneity test	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V<IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV

TABLE II. *Frequency and cover of species in the* Eriophorum spissum-Carex lugens-Arctagrostis latifolia-*Dwarf Shrub Heath Subtype, Carex-Dwarf Shrub Heath Subtype, and Grass-Dwarf Shrub Heath Subtype*

Species	*Eriophorum spissum-Carex lugens-Arctagrostis latifolia-*Dwarf Shrub Heath Subtype			Carex-Dwarf Shrub Heath Subtype											Grass-Dwarf Shrub Heath Subtype			
	Stand 21	Stand 24	Stand 8	Stand 23	Stand 26	Stand 25	Stand 71	Stand 51	Stand 13	Stand 49	Stand 57	Stand 52	Stand 56	Stand 60	Stand 48	Stand 32	Stand 43	Stand 40
Eriophorum spissum Fern.	70^{1}	50^{1}	50^{1}	10^{1}	10^{1}		10^{1}	10^{1}	30^{1}				10^{1}					
Carex lugens Holm.	60^{1}	50^{1}	80^{1}	100^{1}	100^{1}	100^{1}	80^{1}	80^{1}	80^{1}	70^{1}	40^{1}		+					20^{1}
Carex capillaris L.				30^{1}					20^{1}	+	+	+						+
Carex vaginata Tausch.								+				+	50^{1}					+
Carex consimilis Holm.														80^{1}				
Carex scirpoidea Michx.												90^{1}						
Carex membranacea Hook.													40^{1}					
Carex obtusata Lilj.				+														
Luzula confusa Lindeb.	+	20^{1}	30^{1}				10^{1}	10^{1}		70^{1}	40^{1}				50^{1}			10^{1}
Luzula nivalis (Laest.) Beurl.											20^{1}	+	+	50^{1}				
Arctagrostis latifolia (R. Br.) Grieseb.	70^{1}	90^{1}	50^{1}	80^{1}	60^{1}	80^{1}	60^{1}	60^{1}	40^{1}	50^{1}	20^{1}	+	20^{1}		100^{1}	100^{1}	80^{1}	60^{1}
Hierochloe plaina (Sw.) Roem. & Schult.	30^{1}	+	50^{1}			10^{1}	20^{1}		40^{1}	40^{1}	+	20^{1}			30^{1}	40^{1}	+	+
Poa arctica R. Br.			+	10^{1}			60^{1}	20^{1}		60^{1}	30^{1}		10^{1}					
Ledum decumbens (Ait.) Lodd.	100^{1+}	100^{1}	90^{1+}	30^{1}	100^{1+}	100^{1+}	100^{2+}	80^{1}	90^{1}	50^{1}	50^{1}	80^{1}	60^{1}	90^{1+}	80^{1}	90^{1}	100^{1+}	80^{1+}
Vaccinium vitis-idaea L.	100^{1}	100^{1}	90^{1+}	10^{1}	90^{1}	90^{1}	100^{2+}	100^{1}	90^{1+}	70^{1}	80^{1}	20^{1}	70^{1}	100^{1}	100^{1}	90^{1+}	100^{1+}	80^{1+}
Vaccinium uliginosum L.	90^{1}	30^{1}	10^{1}	70^{1}	70^{1}	60^{1}	+	100^{1}	40^{1}	30^{1}	90^{1}	100^{3-}	100^{1}	60^{1+}	20^{1}			70^{1}
Betula nana L. ssp. *exilis* (Sukatch.) Hult.	80^{1+}	70^{1+}	10^{1}	70^{1+}	100^{2}	100^{1+}	100^{2-}	100^{1}	40^{1+}	30^{1}	90^{1}	80^{1+}	100^{1+}		100^{1}	100^{2-}	100^{3-}	100^{3}
Arctostaphylos alpina (L.) Spreng.	90^{1}	100^{1}		100^{1+}		50^{1}	30^{1}	40^{1}	10^{1}	50^{1+}	60^{1}	20^{1}	50^{1}	100^{1+}	70^{1+}	20^{1}	10^{1}	40^{1+}
Cassiope tetragona (L.) D. Don.			40^{1}	60^{1}	10^{1}	20^{1}		100^{1+}	30^{1}	100^{1+}	100^{1+}	70^{1}	100^{1+}	60^{1}			20^{1}	10^{1}
Empetrum nigrum L.	60^{1}	100^{1+}	80^{1+}	40^{1}	60^{1}	50^{1+}	90^{1+}	90^{1}	100^{1+}	10^{1}	40^{1}	100^{1-}	20^{1}	100^{1+}				
Rubus chamaemorus L.	20^{1}													10^{1}		40^{1}		10^{1}
Dryas integrifolia Vahl. (var. *canescens*? Sim.)				50^{1+}						60^{1}	70^{1}	20^{1}	40^{1}					+
Rhododendron lapponicum (L.) Wahl.				20^{1}						10^{1}								10^{1}
Andromeda polifolia L.														30^{1}				
Alnus crispa (Air.) Pursh.	60^{1+}			+	70^{1+}	60^{1+}		+				50^{1+}	70^{1+}				80^{1+}	60^{2}
Salix glauca L.			80^{2-}	70^{1}			+			40^{1}	+					50^{1}	50^{1+}	90^{2}
Salix pulchra Cham.		30^{1}			20^{1}	20^{1}	70^{1+}		10^{1}				+		10^{1}	50^{1}	10^{1}	
Salix phlebophylla Anderss.		+								100^{1+}	30^{1}				20^{1}			
Salix niphoclada Rydb.					30^{1+}				70^{2+}		+		80^{1}		40^{1}		+	
Salix brachycarpa Nutt. var. *mexiae* Ball		+						50^{1+}			90^{1}	60^{1}						
Salix pulchra Cham. var. *palmeri* Ball			10^{1}				30^{1}											
Salix reticulata L.										40^{1}	10^{1}		10^{1}					
Salix arbusculoides Anderss.						+			100^{1+}								20^{1}	+
Salix desertorum Rich.						90^{1}												
Salix richardsonii Hook.									+				+					10^{1}
Salix glauca L. var. *acutifolia* (Hook.) Schn.					10^{1}													
Salix glauca L. var. *aliceae* Ball											+							
Spirea beauverdiana Schneid.															10^{1}	10^{1}		
Potentilla fruticosa L.																		30^{1}
Polygonum bistorta L. ssp. *plumosum* (Small.) Hult.	100^{1}	100^{1}	30^{1}	30^{1}	20^{1}	60^{1}		100^{1}	50^{1}	70^{1}	70^{1}	100^{1}	20^{1}	40^{1}	40^{1}	10^{1}	10^{1}	

TABLE II—*Continued*

Species	*Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtype			Carex-Dwarf Shrub Heath Subtype											Grass-Dwarf Shrub Heath Subtype			
	Stand 21	Stand 24	Stand 8	Stand 23	Stand 26	Stand 25	Stand 71	Stand 51	Stand 13	Stand 49	Stand 57	Stand 52	Stand 56	Stand 60	Stand 48	Stand 32	Stand 43	Stand 40
Pyrola grandiflora Radius			20^1	20^1	40^1	70^1	20^1		70^1		50^1	10^1	90^1					10^1
Stellaria laxmanni Fisch.	+	40^1					30^1				50^1	40^1	60^1			10^1	30^1	+
Petasites frigidus (L.) Fries		10^1	40^1		10^1		50^1	70^1	10^1			10^1					10^1	
Pedicularis capitata Adams		+						+		90^1	60^1		40^1			10^1		
Pedicularis labradorica Panzer	10^1								10^1						10^1			
Pedicularis lanata Willd.			10^1				40^1											
Saussurea angustifolia (Willd.) D. C.		+		60^1	+	20^1	60^1	40^1	60^1	60^1	90^1	30^1	100^1					
Lupinus arcticus Wats.		30^1		70^1			10^1			70^1	80^1		60^1					
Senecio frigidus (Richards.) Hook.		10^1		20^1	+	10^1		+			10^1		10^1					
Antennaria isolepis Greene			10^1						30^1	20^1								
Saxifraga punctata L. spp. *nelsoniana* (D. Don.) Hult.				40^1		20^1		10^1		60^1	50^1		10^1					
Arnica lessingii Greene								+			20^1							
Pyrola secunda L. var. *obtusata* Turex.								40^1										20^1
Rumex acetosa L. spp. *alpestris* (Scop.) Love										+								
Polemonium acutiflorum Willd.				10^1	10^1	20^1			+									
Stellaria longipes Goldie											50^1							
Parrya nudicaulis (L.) Regel. spp. *interior* Hult.											+	+						
Cardamine richardsonii Hult.				+				+										
Anemone richardsonii Hook.									+									
Parnassia kotzebuei C. & S.																		10^1
Lycopodium selago L. var. *appressum* Desv.									10^1									
Equisetum arvense L. var. *boreale* (Bong.) Ledeb.				60^1	30^1													20^1
Equisetum arvense L. var. *boreale* (Bong.) Ledeb. f. *pseudo-varium* Viet.								20^1	+									
Mosses	100^{2+}	100^{2+}	100^{2+}	100^{3-}	100^{3-}	100^3	100^{6-}	100^{6-}	90^{2-}	100^{4+}	100^6	100^{4-}	100^{6-}	100^{4+}	100^{4-}	100^{3-}	100^{5-}	100^{3-}
Lichens	100^{3+}	100^{3-}	100^1	100^1	100^{1+}	100^{2-}	100^{2+}	100^{3-}	80^{1+}	100^{2+}	100^{2+}	100^{1+}	100^{1+}	100^{5+}	100^{2+}	100^{1+}	100^{2+}	100^2
Bare ground			10^1	20^1					10^1									10^1
Total vascular species in quadrats	14	17	18	25	19	20	19	21	21	24	25	17	24	11	15	14	14	19
Average number vascular species per quadrat	9	9	8	11	9	11	10	12	9	13	13	9	10	7	8	7	7	7
Homogeneity-index	84.4	84.4	71.3	71.8	76.7	79.1	77.0	81.7	78.9	71.5	75.4	81.1	78.3	84.3	78.8	74.3	80.0	67.1
Frequency-homogeneity test	V>IV	V>IV	V<IV	V<IV	V>IV	V>IV	V>IV	V>IV	V>IV	V<IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V>IV	V<IV

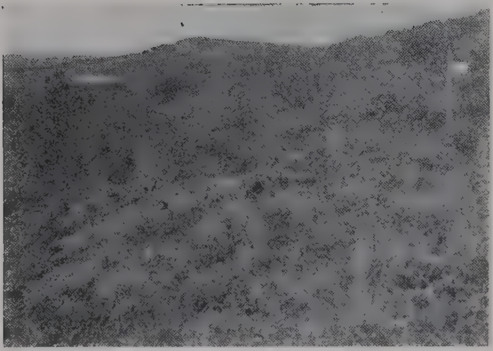

FIG. 1. Stand 20, *Alnus crispa-Eriophorum spissum*—dwarf shrub heath.

no evidence of soil movement or freezing and thawing disturbance. The microrelief with an average of 9 inches, maximum 12 inches, resulted principally from the presence of *Eriophorum* tussocks. Distinctive characteristics of this stand are the high frequency of *Salix pulchra, Eriophorum spissum, Carex lugens,* 5 dwarf shrub species, mosses and lichens.

Stand 62. *Eriophorum spissum*-dwarf shrub heath

This stand, 0.7 miles northwest of Umiat, was located on a gravel terrace of the floodplain. The site was medium moist, almost level and exposed to winds from all directions. The microrelief, average 4 inches and maximum 6 inches, resulted principally from the presence of *Eriophorum* tussocks. There was no evidence of soil movement or disturbance as a result of freezing and thawing. No surface drainage development was apparent. Outstanding characteristics of the vegetation are the high frequency of *Eriophorum spissum,* 3 dwarf shrub species, mosses and lichens.

In general, all the stands of this subtype have the significant species of the dwarf shrub heath complex present with high frequency: *Betula nana* ssp. *exilis, Empetrum nigrum, Ledum decumbens,* and *Vaccinium vitis-idaea.* The exceptions are Stand 53 where *Empetrum nigrum, Ledum decumbens* and *Vaccinium vitis-idaea* have medium frequency; Stand 10 where *Empetrum nigrum* is absent; Stand 62 where *Betula nana* ssp. *exilis* and *Empetrum nigrum* are merely present or of low frequency; and Stands 65 and 69 with medium frequency of *Empetrum nigrum.* Other dwarf shrub heath species and associates in the order of decreasing frequency in the stands are *Arctostaphylos alpina, Cassiope tetragona, Vaccinium uliginosum, Rubus chamaemorus, Andromeda polifolia* and *Dryas integrifolia* (var. *canescens*?). These are present in different combinations in the various stands. There is no apparent consistence of association in frequency or in presence of any 2 or more species within this group or with the previously mentioned group of dwarf shrub heath species.

Alnus crispa is present in only 8 of the 22 stands, having high frequency in only Stands 20 and 3. Of the willows, *Salix pulchra* is the most predominant, being present in 9, having a high frequency in 3, and moderately high frequency in 1. Two stands, 58 and 53, have 5 species of *Salix* present, both of which are the only stands with both *Salix niphoclada* and *S. reticulata.* Stands 62, 65 and 69 have neither *Alnus crispa* nor a species of *Salix* present.

In almost all stands, *Eriophorum spissum* has a frequency of 70 to 100% and low to moderately high cover with the exception of Stand 69 where the frequency is only 40% and Stand 27 where it is absent. In this last stand, however, *Eriophorum vaginatum* has a frequency of 70% and low cover. Both *Carex lugens* and *C. consimilis* are variable in frequency and usually the cover is low.

Arctagrostis latifolia is more generally present in the stands than the other species of grasses. All grasses usually have low frequency and only Stands 73 and 41 have a frequency rating as high as 40% and this for 1 species of grass.

Polygonum bistorta ssp. *plumosum* is the forb most prevalent in the stands. The frequency varies from low to high in 15 stands and it is absent in the other stands.

All stands are homogeneous by the frequency-homogeneity test with the exception of Stand 74 where the ratio of class V to class IV frequencies is 4 to 5. With this test, Stand 70 with a ratio of 8 to 0 has the greatest ratio because of the 100% frequency of *Eriophorum spissum, Betula nana* ssp. *exilis, Ledum decumbens, Vaccinium vitis-idaea, V. uliginosum, Empetrum nigrum, Salix pulchera* and *Carex lugens.* It is noteworthy that there is good agreement of the frequency-homogeneity test with the homogeneity-index. The homogeneity-index of 89.0 for this stand is one of the highest. It also has a relatively high total number of 18 vascular species in quadrats and a high average number of 10 vascular species per quadrat. Stand 3 with a homogeneity-index of 92.2 has the highest index and the frequency-homogeneity ratio of 7 to 1 is also one of the highest. This stand has a total number of 14 vascular species in the quadrats, less than Stand 70. However, the 2 stands have an average number of species per quadrat of 9 and 10 respectively.

Stand 74, mentioned above, is heterogeneous by the frequency-homogeneity test due to the class IV frequency of *Eriophorum spissum, Betula nana* spp. *exilis, Vaccinium vitis-idaea, V. oxycoccus* and *Salix fuscescens* var. *reducta* and the class V frequency of *Ledum decumbens, Empetrum nigrum, Andromeda polifolia* and *Carex lugens.* The total number of vascular species in quadrats is 13, relatively low, and the average number of vascular species per quadrat of 9 is relatively high. Although this stand is heterogeneous by the frequency-homogeneity test, it has a higher homogeneity-index than some other stands which are homogeneous by the frequency-homogeneity test. This is due to the particular characteristics of the 9 species with the highest frequencies, all with frequencies of 70% or more but 5 of these have frequencies in class IV. In several other stands with a comparable homogeneity-index and average number of vascular species per quadrat, a smaller number of species with highest frequencies are in class IV, instead more occur with frequencies of 60% or less.

2. *Eriophorum spissum-Carex lugens-Arctagrostis latifolia-Dwarf Shrub Heath Subtype.*—Three stands are included in this subtype on the basis of nearly equal frequency and cover of *Eriophorum spissum, Carex lugens* and *Arctagrostis latifolia,* high frequency of dwarf shrub heath and associated species, especially *Ledum decumbens* and *Vaccinium vitis-idaea,* and varying frequency of *Empetrum nigrum, Betula nana* ssp. *exilis* and *Vaccinium uliginosum.* This subtype has a limited occurrence and was found only on the upland.

Stand 21. *Alnus crispa-Eriophorum spissum-Arctagrostis latifolia-Carex lugens*-dwarf shrub heath

This stand, about 1.3 miles north of Umiat, was located midway up the south-facing slope which extended from the floodplain to the upland. The dry slope was approximately 8°. The site was protected from north winds. The lateral micro-relief averaged 8 inches and the maximum was 12 inches. The micro-relief on the slope was greater, it had an average of 10 inches and maximum of 20 inches. Slump holes and mounds with abrupt down-slope faces resulting from soil movement were numerous in occurrence. Surface drainage was well-developed, consisting of microchannels varying in form from cracks to channels, well rounded in cross section, and with a maximum width of 12 inches and an average of 7 inches. Stands resembling this stand occurred on similar sites of the slope. The characteristics of this stand (Table II) are the high frequency of *Eriophorum spissum, Arctagrostis latifolia, Carex lugens,* 4 dwarf shrub species, *Polygonum bistorta* ssp. *plumosum,* mosses and lichens.

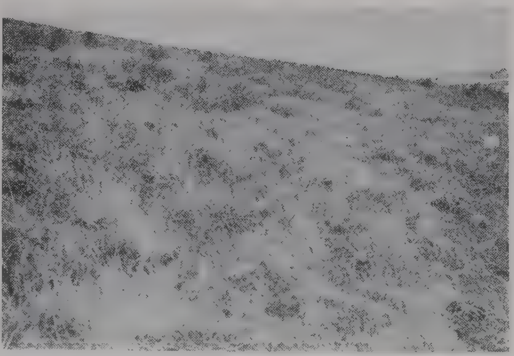

FIG. 2. Stand 21, *Alnus crispa-Eriophorum spissum-Arctagrostis latifolia-Carex* lugens—dwarf shrub heath.

The frequencies of *Eriophorum spissum, Carex lugens,* and *Arctagrostis latifolia* are more similar in Stand 21 than in the other 2 stands. *Vaccinium vitis-idaea, Ledum decumbens, Empetrum nigrum,* and *Betula nana* spp. *exilis* are present with medium to high frequency with the exception of *Betula nana* spp. *exilis* which has low frequency in Stand 8.

Alnus crispa in Stand 21 with no species of *Salix* present, *Salix glauca* in Stand 8 with no *Alnus crispa,* and the lack of *A. crispa* and the low frequency of *Salix pulchra* and presence of 2 other *Salix* spp. in Stand 24 are outstanding characteristics of the respective stands.

Polygonum bistorta ssp. *plumosum* has high frequency in Stands 21 and 25 but low frequency in Stand 8. Stand 21 is very poor in forb species, only 3 are present. Stand 24 with a total of 8 has the largest number of forbs.

Although the mosses and lichens have high frequency, the cover is relatively low.

Stands 21 and 24 with 84.4 have the highest homogeneity-indices and by the frequency-homogeneity test both are homogeneous. Stand 24 has the higher frequency-homogeneity ratio, 6 to 1; Stand 21 has 5 to 3. In Stand 24, the 6 species in frequency class V, *Arctagrostis latifolia, Ledum decumbens, Vaccinium vitis-idaea, Empetrum nigrum, Arctostaphylos alpina* and *Polygonum bistorta* spp. *plumosum,* account for 8.5 times more cover than the 1 species, *Betula nana* ssp. *exilis,* in frequency class IV. In Stand 24, the total number of vascular species in quadrats is 17, the highest of the 3 stands, and the average number of vascular species per quadrat is 9, the same as in Stand 21.

Stand 8 is heterogeneous by the frequency-homogeneity test, the ratio being 2 to 3, and the homogeneity-index, 71.3, is the lowest of the 3 stands. The species in frequency class IV, *Salix glauca, Carex lugens* and *Empetrum nigrum,* have a cover approximately 2 times that of the species in frequency class V. The total number of vascular species in quadrats is 18, the highest of the 3 stands, and the average number of vascular species per quadrat is 8, the lowest of the 3 stands.

3. *Carex-Dwarf Shrub Heath Subtype.*—The results of the analysis of 11 stands are grouped in Table II on the basis of high or relatively high frequency of *Carex* spp.; the frequency of the *Carex* spp. of the respective stands being higher than that of any grass species, and the absence or low frequency of *Eriophorum* spp. Since *Carex lugens* in Stand 57, with a frequency of 40%, has a higher frequency than either *Arctagrostis latifolia* or *Poa arctica,* it is included in this subtype. In the first 8 stands, *Carex lugens* has the highest frequency but it is replaced by other species of Carex in the remaining stands. Dwarf shrub heath species and associates are present in varying combinations. The Carex-Dwarf Shrub Heath Subtype is more limited in occurrence than the Eriphorum Tussock-Dwarf Shrub Heath Subtype.

Stand 25. *Salix desertorum-Alnus crispa-Carex lugens*-dwarf shrub heath

The stand, 1.3 miles north of Umiat, was located on the upper portion of the south-facing slope which extended from the upland to the floodplain. The slope was approximately 12°. It had a limited amount of protection from north winds and the site was medium moist. The microrelief, average 16 inches and maximum 30 inches, resulted from the presence of mounds which were round or elongate, the latter form being parallel to the direction of the slope. The surface drainage was well-developed. The vegetation characteristics of the stand (Table II) are the high or moderately high frequency of *Carex lugens, Salix desertorum,* 3 dwarf shrub species, *Arctagrostis latifolia,* mosses and lichens.

Stand 71. *Salix pulchra-Carex lugens*-grass dwarf shrub heath

The stand, about 0.8 mile west-northwest of Umiat, was on a level portion of the low terrace. The site was medium moist. There was no apparent development of surface drainage and no evidence of soil movement. The microrelief, average 6 inches, maximum 12 inches, resulted from the presence of moss mounds which averaged 15 inches in diameter. The vegetation is characterized by the high frequency of 3 dwarf shrub species, mosses and lichens and the moderately high frequency of *Carex lugens, Empetrum nigrum* and *Salix pulchra.*

FIG. 3. Stand 25, *Salix desertorum-Alnus crispa-Carex lugens*—dwarf shrub heath.

Empetrum nigrum, Ledum decumbens, Vaccinium vitis-idaea and *V. uliginosum* are present in all of the stands analyzed in this subtype. *Betula nana* ssp. *exilis* is not present in Stand 60, *Arctostaphylos alpina* is not present in Stand 26 and *Cassiope tetragona* is not present in Stand 71. *Dryas integrifolia* (var. *canescens*?) is present in 5 stands, *Rhododendron lapponicum* in 2, *Rubus chamaemorus* in 1 and *Andromeda polifolia* in 1. Usually more than 3 of these species are present in each stand with high or moderately high frequency. Stand 49 has 9 of these 11 species present but only *Cassiope tetragona* and *Vaccinium vitis-idaea* are high in frequency.

A species of *Carex* is present in each of the stands and its frequency is higher than the frequency of any one species of grass. *Carex lugens* is present with high frequency in the first 7 stands and *C. capillaris* with low frequency is also present in 2 of these stands.

One or more species of grass are present in each stand with the exception of Stand 60. The frequency of *Arctagrostis latifolia* is usually equal to or higher than that of other species of grass. *Eriophorum spissum* is present in 6 stands, the frequency being low.

Alnus crispa is present in 4 stands with medium to moderately high frequency and occurs in 2 additional stands without cover rating. *Salix reticulata* is present in 3 stands with low to medium frequency and *S. phlebophylla* is present in 2 of these stands with higher frequency. Ten other species of *Salix* are present in 10 of the stands in various combinations and frequencies, at least one species being present with medium to high frequency. In Stand 60, there is neither *Alnus crispa* nor a species of *Salix* present.

A total of 20 forbs is found in these 11 stands, 2 species, *Polygonum bistorta* ssp. *plumosum* and *Saussurea angustifolia,* are present in 10 stands but only the first of these species is present in Stand 60. *Lupinus arcticus,* in this subtype, is present in 5 stands.

In Stand 13, the frequency of mosses is 90% and of lichens is 80%; the cover is low for both. In all other stands, the frequency of mosses and lichens is 100%; the cover of mosses is from medium to high and of lichens is generally low. However, the cover of lichens is medium in Stand 51 and moderately high in Stand 60.

The homogeneity-index of 81.7 for Stand 51 is next to the highest of the 11 stands, and the frequency-homogeneity test indicates homogeneity by a ratio of 6 to 3. This is especially significant since 21 vascular species are found in the 10 quadrats with an average of 12 per quadrat, and 9 of these have a frequency of 70% or greater. Five dwarf shrub heath species and associates, *Empetrum nigrum, Vaccinium vitis-idaea, Betula nana* ssp. *exilis, Vaccinium uliginosum, Cassiope tetragona,* and one forb, *Polygonum bistorta* ssp. *plumosum,* are in frequency class V. This group of species has a cover aproximately 2.5 times that of the group of species in frequency class IV. Stand 60 with 84.4 has the highest homogeneity-index and its frequency-homogeneity ratio of 4 to 1 is also the highest. It has about one-half the total number of vascular species and slightly more than one-half the average number per quadrat compared to Stand 51. Stand 60 also has the lowest total number of vascular species in quadrats and the lowest average number of species per quadrat of the 11 Carex-dwarf shrub heath stands, so it cannot be considered typical for the subtype.

The homogeneity-index of 71.5 in Stand 49 is the lowest in this subtype and the frequency-homogeneity ratio of 3 to 5 is 1 of the lowest, the test indicating it to be heterogeneous. Stand 23 has a homogeneity-index of 71.8 and a frequency-homogeneity ratio of 2 to 5, thus being the second of 2 heterogeneous stands. Stands 49 and 23 have a high total number of vascular species in the 10 quadrats, 24 and 25 respectively, and a high average number of vascular species per quadrat, 13 and 11 respectively. In Stand 49, the cover of the species in frequency class V is slightly greater than the cover of the species in class IV.

4. *Grass-Dwarf Shrub Heath Subtype.*—The most characteristic features of this subtype, in contrast to the preceding subtype, are the high to medium frequency of *Arctagrostis latifolia,* accompanied by the low frequency or absence of *Carex* spp., absence of *Eriophorum* spp., and presence of 5 or more dwarf shrub heath and associate species, 2 of which as a minimum have high frequency. Two of the 4 stands are discussed in detail.

Stand 48. *Arctagrostis latifolia*-dwarf shrub heath

This stand, 1.6. miles northwest of Umiat, was located on a north-northeast slope of 11°. Since the stand was just below the top of a ridge there was no protection from north-northeast winds and only slight protection from winds from other directions. The site was medium moist. Surface drainage was channeled into cracks with abrupt sides and broad microchannels 12 inches wide with gentle side slopes. Frost scars were infrequent. Soil movement was indicated by the frequent occurrence of mounds which had an average diameter of 2 feet. The microrelief, resulting principally from the presence of the mounds, averaged 10 inches with a maximum of 16 inches. The vegetation (Table II) is characterized by the high frequency of *Arctagrostis latifolia,* 5 dwarf shrub species, mosses and lichens.

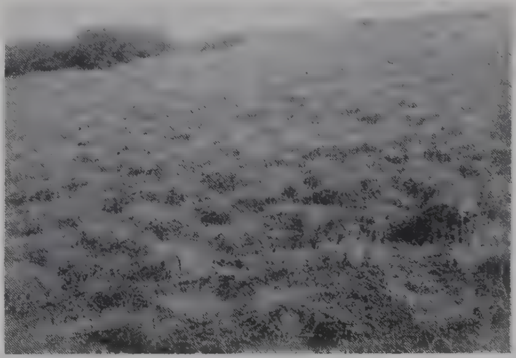

FIG. 4. Stand 48, *Arctagrostis latifolia*—dwarf shrub heath.

Arctagrostis latifolia and *Hierochloe alpina* are the only grass species present in these Grass-Dwarf Shrub Heath Subtype stands. *Arctagrostis latifolia* is present with medium to high frequency and its frequency is always higher than that of *Hierochloe alpina.*

The dwarf shrub heath and associated species are well-represented, especially by *Vaccinium vitis-idaea, Ledum decumbens, Arctostaphylos alpina* and *Betula nana* ssp. *exilis.* The last species, however, has a frequency of only 10% in Stand 40. *Vaccinium uliginosum, Rubus chamaemorus, Cassiope tetragona, Rhododendron lapponicum,* and *Dryas integrifolia* (var. *canescens*?)

are present in varying combinations, usually with low to moderately low frequency.

Alnus crispa is present only in Stands 43 and 40 with moderately high and medium frequency respectively. *Salix glauca* is present in 3 stands with high to medium frequency; *S. pulchra* is present in 3 stands with low to medium frequency; 4 other species of *Salix* are present in various combinations from mere presence to medium frequency. Mosses and lichens have high frequency in all stands. The cover of mosses is from medium to moderately high and the cover of lichens is moderately low.

Carex spp. are present only in Stand 40, *Carex lugens* has a low frequency and *C. capillaris* and *C. vaginata* are present without cover rating. *Eriophorum spissum* occurs in Stand 48.

Eight species of forbs are present in varying combinations with low to medium frequency.

Two species, *Spirea beauverdiana* and *Potentilla fruticosa,* which are not abundant in this area, occur infrequently in this subtype, the former in 2 stands, the latter in only 1 stand.

Stand 32 has a frequency-homogeneity ratio of 4 to 0, resulting from the presence of *Betula nana* ssp. *exilis, Arctagrostis latifolia, Vaccinium vitis-idaea* and *Ledum decumbens.* These species with mosses dominate the stand. The frequency-homogeneity ratio of this stand is the highest in this subtype; of the 3 stands which are homogeneous by this test, Stand 32 has the lowest homogeneity-index.

Stand 40 is heterogeneous by a ratio of 1 to 3, with the frequency-homogeneity test and its homogeneity-index of 67.1 is the lowest. *Salix glauca* is the chief dominant with *Alnus crispa* next; these 2 species probably are factors in causing variation in the frequency and cover of the dwarf shrub heath and associated species. The ratio of the total number of vascular species in quadrats to the average number of vascular species per quadrat of 19 to 7 is the highest such ratio in this subtype and this may have contributed to the heterogeneity.

Discussion of the Dwarf Shrub Heath Type.—The Dwarf Shrub Heath Type has a very extensive distribution on the upland and less extensive distribution on the high terrace of the floodplain.

Dwarf shrub heaths and associated species characterize the type. The most important species are *Betula nana* ssp. *exilis, Ledum decumbens, Vaccinium vitis-idaea* and *Empetrum nigrum.* The last species tends to be more variable with respect to presence and frequency than the first 3. Other dwarf shrub heaths and associated species occur in varying combinations and with varying frequencies. The frequencies of mosses and lichens are consistently high.

If *Alnus crispa* and a species of *Salix* are both present in the same stand, there is a tendency for one to have a significantly greater frequency than the other. There are very few exceptions where *Alnus crispa* and a species of *Salix* occur in the same stand with approximately equally high frequency.

Polygonum bistorta ssp. *plumosum* has consistently higher frequency than any other forb.

The type is divided into 4 subtypes on the basis of the relative frequencies of *Eriophorum, Carex,* and grass species. In the Eriophorum Tussock-Dwarf Shrub Heath Subtype the frequency of *Eriophorum* spp., usually *E. spissum,* is generally greater than that of the *Carex* spp., usually *C. lugens,* and the frequency of the *Carex* in turn is greater than that of *Arctagrostis latifolia.* This subtype includes the largest number of dwarf shrub heath species and associates. *Betula nana* ssp. *exilis, Ledum decumbens, Vaccinium vitis-idaea* and *Empetrum nigrum* usually have high frequencies. Only 1 stand out of 22 is heterogeneous by the frequency-homogeneity test.

The *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtype is characterized by equal or nearly equal frequencies of the 3 named species. Fewer species of dwarf heath and associates are present; only *Ledum decumbens* and *Vaccinium vitis-idaea* have consistently high frequencies; *Betula nana* ssp. *exilis* is variable. One of the 3 stands is heterogeneous.

In the Carex-Dwarf Shrub Heath Subtype, the *Carex* spp., usually *C. lugens,* has a higher frequency than *Arctagrostis latifolia* which has a higher frequency than *Eriophorum spissum,* if the latter is present. Fewer dwarf shrub heath and associated species are present than in the above mentioned subtypes. *Ledum decumbens, Vaccinium vitis-idaea* and *Betula nana* ssp. *exilis* have a greater tendency for high frequencies than in the *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtype but less than in the Eriophorum Tussock-Dwarf Shrub Heath Subtype. Two of the 11 stands are heterogeneous.

The Grass-Dwarf Shrub Heath Subtype is characterized by a grass species, usually *Arctagrostis latifolia,* which has a higher frequency than the species of Carex and *Eriophorum spissum,* if either of the latter is present. *Betula nana* ssp. *exilis, Vaccinium vitis-idaea* and *Ledum decumbens* have consistently high frequencies; *Empetrum nigrum*

TABLE III. *Frequency and cover of species in the Frost-Scar Collective Type, Salix Type,* Alnus crispa *Type, and* Carex aquatilis-*Marsh Type*

Species	Frost-Scar Collective Type				Salix Type		*Alnus crispa* Type		*Carex aquatilis*-Marsh Type		
	Stand 4	Stand 5	Stand 16	Stand 22	Stand 11	Stand 42	Stand 36	Stand 78	Stand 55	Stand 64	Stand 67
Arctostaphylos alpina (L.) Spreng.	40^1	70^1	80^1	80^{1+}				10^1			
Cassiope tetragona (L.) D. Don.	10^1	80^1	60^1								
Empetrum nigrum L.			100^1	100^1	10^1	20^1		10^1			
Vaccinium vitis-idaea L.			80^1	90^{1+}		40^1	10^1				
Betula nana L. ssp. *exilis* (Sukatch.) Hult.			80^1	70^1	70^{1+}		10^1			10^1	20^1
Ledum decumbens (Ait.) Lodd.			80^1	70^1		40^1	10^1	10^1			
Vaccinium uliginosum L.			80^1	40^1	20^1	30^1	20^{1+}	50^1			
Dryas integrifolia Vahl. (var. *canescens*? Sim.)	100^{2+}	100^{2+}									
Rhododendron lapponicum (L.) Wahl.	10^1	10^1									
Rubus chamaemorus L.					10^1	90^{1+}					
Andromeda polifolia L.											50^1
Alnus crispa (Air.) Pursh					20^2		100^{4+}	100^{5+}			
Salix pulchra Cham.		60^{1+}		10^1		100^{2+}	80^2				
Salix phlebophylla Anderss.				90^{1+}							
Salix glauca L. var. *glabrescens* (Anderss.) Schn.					100^{3-}			100^{3-}			
Salix glauca L.	70^1						10^1				
Salix brachycarpa Nutt. var. *mexiae* Ball			30^1								
Salix niphoclada Rydb.				30^{1+}							
Salix arbusculoides Anderss.						+		50^{2+}			
Salix fuscescens Anderss. var. *reducta* Ball									+	+	90^1
Salix desertorum Rich.						20^1		10^1			
Salix alaxensis (Anderss.) Cov.					+						
Salix pulchra Cham. var. *palmeri* Ball			+								
Caltha palustris L. var. *arctica* (R. Br.) Huth								20^1	60^1	+	100^{1+}
Eriophorum spissum Fern.				10^1	10^1	20^1					
Eriophorum angustifolium Roth.									50^1	20^1	50^1
Carex scirpoidea Michx.		90^1									
Carex glacialis Mack.	80^1										
Carex lugens Holm				40^1	50^1						
Carex capillaris L.				10^1							
Carex consimilis Holm						80^1					
Carex aquatilis Wahl.								60^1	100^{4-}	100^{4-}	100^3
Luzula confusa Lindeb.			50^1	30^1		10^1					
Luzula nivalis (Laest.) Beurl.					10^1						
Arctagrostis latifolia (R. Br.) Grieseb.			40^1	80^1	40^1	60^1	90^1	90^{1+}	80^1		80^1
Hierochloe alpina (Sw.) Roem. & Schult.			60^1	40^1	+	10^1					
Festuca altaica Trin.	20^1	10^1									
Poa arctica R. Br.				30^1	30^1	60^1					
Pedicularis lanata Willd.	70^1	50^1	10^1	40^1							30^1
Lupinus arcticus Wats.	90^1	90^1	30^1								
Polygonum bistorta L. ssp. *plumosum* (Small.) Hult.		60^1	70^1	100^1		10^1					
Stellaria laxmannii Fisch.		30^1	20^1	60^1	+	20^1	10^1	+	80^1		
Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch.	40^1	50^1						30^1	90^1		
Petasites frigidus (L.) Fries.					100^{1+}	50^1	10^1	50^1			
Saxifraga cernua L.	10^1				20^1	40^1	20^1	30^1	90^1		
Silene acaulis L. var. *exscapa* DC.	10^1	30^1									
Pyrola grandiflora Radius.	+	30^1				60^1	50^1	80^{1+}			
Antennaria isolepis Greene	50^1										
Arnica alpina (L.) Olin & Ladon ssp. *angustifolia* (Vahl.) Maguire	+	20^1									
Pedicularis capitata Adams.			20^1		10^1						
Valeriana capitata Pall.					70^1						
Polemonium acutiflorum Willd.								30^1			
Cardamine pratensis L.									30^1		
Pedicularis labradorica Panzer										20^1	
Tofieldia pusilla (Michx.) Pers.		20^1									
Potentilla hookeriana Lehm.	+	10^1									
Saxifraga punctata L. ssp. *nelsoniana* (D. Don.) Hult.				10^1				20^1			
Saussurea angustifolia (Willd.) D. C.	+										
Castilleja pallida (L.) Spreng.		+									
Oxytropis sp.		+									
Equisetum arvense L. var. *boreale* (Bong.) Ledeb. f. *pseudo-varium* Viet.					40^1	10^1	20^1	50^1			
Mosses	100^{1+}	100^{1+}	100^1	100^{2+}	100^6	100^{4+}	90^{1+}	100^{3+}	100^{2+}	100^1	100^{4+}

TABLE III—*Continued*

Species	Frost-Scar Collective Type				Salix Type		*Alnus crispa* Type		*Carex aquatilis*-Marsh Type		
	Stand 4	Stand 5	Stand 16	Stand 22	Stand 11	Stand 42	Stand 36	Stand 78	Stand 55	Stand 64	Stand 67
Lichens	70^{1}	100^{1}	100^{1}	100^{2+}	60^{1}	20^{1}	....	50^{1}	....	....	....
Bare ground	100^{2+}	100^{2-}	100^{3+}	20^{1}	....	....	100^{6}	100^{5-}	....	100^{4+}	....
Water	....	....	....	....	....	....	....	....	50^{2+}	....	100^{4+}
Total vasc. spp. in quadrats	14	17	17	22	16	19	13	18	8	4	9
Average no. vasc. spp. per quadrat	6	8	9	11	6	7	4	8	6	1	6
Homogeneity-index	75.0	62.5	76.7	78.2	75.0	64.3	80.0	72.5	83.3	100.0	78.3
Freq.-homogeneity test	V<IV	V>IV	V<IV	V=IV	V>IV	V=IV	V>IV	V>IV	V=IV	V>IV	V>IV

is not present. There are fewer species of dwarf shrub heath and associates than in the Eriophorum Tussock-Dwarf Shrub Heath Subtype but more than in the other 2 subtypes. One of the 4 stands is heterogeneous.

II. Frost-scar collective type

This type is called collective because of the variety of microstands which occurred in juxtaposition to one another. In the limited time available for field study, it was not possible to segregate and classify the various microstands. On aerial photographs and from the air these areas, marked by frost scars, are distinct in contrast to adjoining vegetation, so it is important in photographic interpretation that they be described and classified. Analyses are made of 4 stands, 2 of which are discussed in detail.

On the basis of phytosociologic analysis (Table III) Stands 4 and 5 form 1 subtype and Stands 16 and 22 form another subtype.

Stand 4. *Dryas integrifolia* (var. *canescens*?) —*Lupinus arcticus*

This stand, 2.0 miles northeast of Umiat, was located on the south side of the crest of a ridge. The slope of the upper portion of the stand was 4° and of the lower portion 9°. The site was dry with well-developed surface drainage consisting of channels that averaged 1 foot deep. The area was exposed to winds from all directions. Elongated mounds lying parallel with the direction of the slope were indicative of soil movement. There were frost scars on almost all mounds. The microrelief averaged 1 foot with a 2 foot maximum. The vegetation was essentially restricted to the channels between the mounds; infrequently, it was present on the perimeters of the relatively flat bare tops of the mounds. Plants occurring here were usually the same species as in the depressions. The vegetation characteristics (Table III) are the high frequency of *Dryas integrifolia* (var. *canescens*?), *Lupinus arcticus*, and *mosses* and the medium frequency of *Salix glauca*, *Carex glacialis*, *Arctostaphylos alpina*, 3 forb species, and lichens.

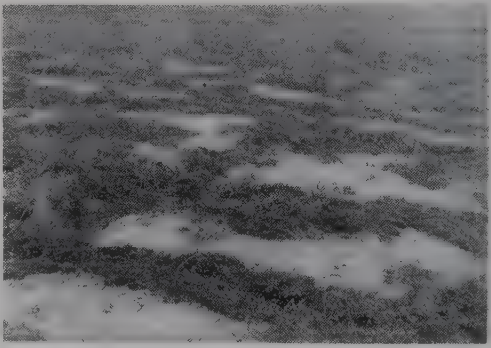

FIG. 5. Stand 4, *Dryas integrifolia* (var. *canescens?*)-*Lupinus arcticus*.

Stand 22. *Salix phlebophylla*-dwarf shrub heath

This frost scar area, 1.4 miles north-northeast of Umiat, occurred about half-way up the slope from the floodplain to the upland. The south-facing slope of 7° was protected from north winds. The site was medium moist although the surfaces of the frost scars were dry when examined. The microrelief averaged 8 inches with a maximum of 12 inches and resulted from the presence of the mounds which averaged 2.5 feet in diameter. The presence of the mounds with their more abrupt down-slope faces and gentle up-slope faces indicated soil movement. The surface drainage was well-developed, the microchannels ranging from 2 inches deep and V-shape in cross-section to 12 inches deep and U-shape in cross-section. The characteristics of the vegetation are the moderately high frequency of *Salix phlebophylla*, 6 dwarf shrub species, mosses and lichens.

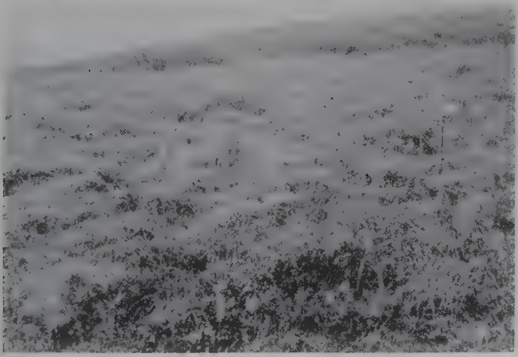

FIG. 6. Stand 22, *Salix phlebophylla*—dwarf shrub heath.

Discussion of the Frost-Scar Collective Type.—Even though stands may differ greatly in composition, phytosociologic analysis yields data which form a basis for grouping the stands into categories. In this Frost-Scar Collective Type, the 4 stands can be classified into 2 distinctive subtypes. Stands 4 and 5 are in the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype, and Stands 16 and 22 in the Dwarf Shrub Heath Frost-Scar Subtype.

The *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype is characterized by the high frequency of the named species; *Salix glauca* and *Carex glacialis* have high frequency in Stand 4; *S. pulchra* and *C. scirpoidea* have high frequency in Stand 5; *Lupinus arcticus,* mosses, and lichens have high frequency in both stands. In this subtype, the species of the dwarf shrub heath and associated group are *Arctostaphylos alpina, Cassiope tetragona,* and *Rhododendron lapponicum.* There are several species of forbs and one species of grass, *Festuca altaica.* Only Stand 5 is homogeneous by the frequency-homogeneity test and that by the small ratio of 3 to 2. However, the homogeneity-index of this stand is lower than in Stand 4 which is heterogeneous by the frequency-homogeneity test.

The Dwarf Shrub Heath Frost-Boil Subtype is characterized by the presence and high frequency of *Empetrum nigrum, Vaccinium vitis-idaea, Arctostaphylos alpina, Betula nana* ssp. *exilis* and *Ledum decumbens;* low to high frequency of *Salix* spp.; high frequency of *Arctagrostis latifolia* and *Hierochloe alpina;* high frequency of mosses and lichens; relatively few species of forbs. In Stand 16, there is a much greater area and higher frequency of bare ground as a result of frost scars, indicative of more intensive and extensive freezing disturbance than in Stand 22. The vegetative cover in Stand 22 is approximately 15 times greater than in Stand 16. The total number of vascular species in quadrats and the average number of vascular species per quadrat are slightly less in Stand 16 than in Stand 22.

Stand 22 has a vegetative cover approximately 9 times greater than that of Stand 4. Each of the 2 stands has comparable degrees of heterogeneity. The composition of Stand 22 includes approximately 55% more vascular species in the total number in the quadrats and approximately 80% more vascular species per quadrat than Stand 4.

III. Salix Type

Two stands of the *Salix* Type were analyzed, both were located on the upland and on wet sites.

Stand 11. *Salix glauca* var. *glabrescens-Petasites frigidus*

The stand was restricted to a well-defined small drainage channel on the upland, 1.9 miles north-northeast of Umiat. Water was flowing in the channel during the entire summer. The gradient of the channel was 4° to the east. Although the site was constantly wet, the water was not stagnant. The stand and surrounding communities were exposed to winds from all directions. The microrelief, resulting principally from the presence of moss mounds, mostly *Sphagnum* spp., which had formed or were in the process of forming, reached a maximum of 10 inches and an average of 7 inches. This stand was typical of many small upland drainage channels. Characteristics of this stand (Table III) are the high frequency of *Salix glauca* var. *grabrescens, Rubus chamaemorus, Petasites frigidus* and mosses, especially *Sphagnum* spp.

Discussion of Salix Type.—The outstanding characteristics of the Salix Type (Table III) are the high frequency and medium cover of *Salix*

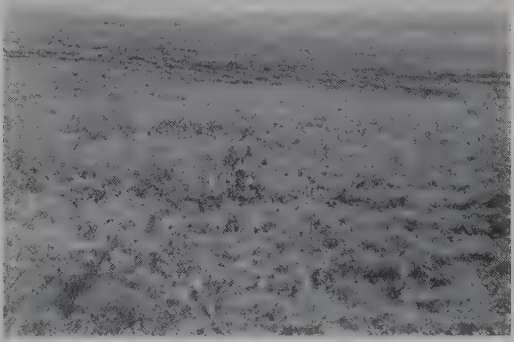

FIG. 7. Stand 11, *Salix glauca* var. *glabrescens-Petasites frigidus.*

glauca var. *glabrescens* and *S. pulchra* and the high frequency and cover of mosses. One or two additional species of *Salix* also occur.

One species of Carex occurs in each stand, *Carex lugens* with medium frequency in Stand 11 and *C. consimilis* with high frequency in Stand 42. *Eriophorum spissum* occurs in both stands with low frequency. One species of Luzula is present in each stand with low frequency, *L. confusa* in Stand 42 and *L. nivalis* in Stand 11. *Arctagrostis latifolia* and *Poa arctica* occur in both stands with low to medum frequency.

The dwarf shrub heath and associated species are present in each stand in varying combinations and frequencies; *Vaccinium uliginosum* and *Empetrum nigrum* are the only species which are present in both stands.

Petasites frigidus occurs with high frequency in Stand 11 and *Pyrola grandiflora* has a medium frequency in Stand 42; these species have the highest frequencies of the forbs in the respective stands.

With the frequency-homogeneity test, Stand 11 is homogeneous and Stand 42 is heterogeneous; the homogeneity-index of Stand 11 is higher than that of Stand 42.

IV. Alnus crispa Type

Two stands of the *Alnus crispa* Type were analyzed, one was on the upland and the other was on the low terrace of the Colville River floodplain.

Stand 36. *Alnus crispa*

The stand was situated in a draw, with a V-shaped cross section, on the south-facing slope which extended from the upland to the floodplain, 1.6 miles north-northeast of Umiat. The stream in the draw was intermittent in flow; the gradient varied from 10° to 15°, descending as a series of steps. The vegetation characteristics (Table III) are the high frequency of *Alnus crispa* which averages 6 feet in height, *Salix pulchra* and *Arctagrostis latifolia,* the latter was uniformly scattered throughout the stand beneath the openings in the crown canopy of high shrubs.

Discussion of Alnus crispa Type.—In both stands, *Alnus crispa* is the principal dominant as a result of high frequency and cover and in each stand one species of *Salix* is a secondary dominant; *S. pulchra* in Stand 36 and *S. glauca* var. *glabrescens* in Stand 78.

The frequency of mosses is high in both stands; the cover is low in Stand 36 and moderately low in Stand 78. Lichens are present only in Stand 78 with medium frequency and low cover. A high percentage of the ground in each stand is bare.

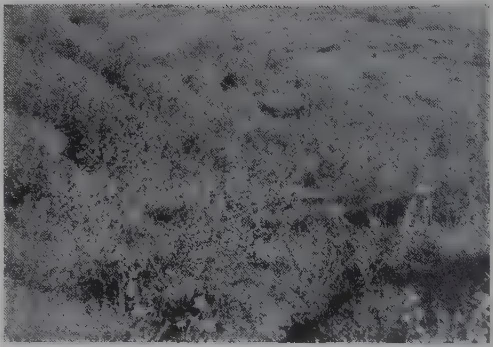

FIG. 8. Stand 36, *Alnus crispa.*

Arctagrostis latifolia has high frequency in both stands. *Carex aquatilis* has medium frequency in Stand 78.

Only 5 species of dwarf shrubs and associates occur in the stands. Their frequencies are low except in the case of *Vaccinium uliginosum* which has medium frequency in Stand 78.

Pyrola grandiflora has the highest frequency of forb species in both stands. There are 3 additional species of forbs in Stand 36 and 6 in Stand 78. *Equisetum arvense* var. *boreale* f. *pseudovarium* occurs with low to medium frequency.

Both stands are homogeneous by the frequency-homogeneity test, Stand 78 having the higher ratio of 3 to 1, but the homogeneity-index of Stand 78 is lower than that of Stand 36 as a result of a greater average number of vascular species per quadrat and dominance of *Alnus crispa* and *Salix glauca* var. *glabrescens.*

V. Carex aquatilis-Marsh Type

Three stands of the *Carex aquatilis*-Marsh Type were analyzed, one was on the upland and the others were on the floodplain.

Stand 55. *Carex aquatilis*-marsh

This marsh, approximately 2.5 miles north-northwest of Umiat, was restricted to a stream channel which was flat in cross section, of low gradient, and flowing to the east. Throughout the entire channel, which varied from 10 to 25 feet in width, water was flowing slowly in numerous shallow channels. These averaged 4 inches in width. The average microrelief was 1 inch, maximum 5 inches. There was no indication of either horizontal or vertical soil movement or freezing disturbance. About 100 yards downstream from the sample area was the head of a thaw gully which was at least 25 feet deep and which had been gradually working upstream in the channel. Examination of the gully face showed numerous

FIG. 9. Stand 55, *Carex aquatilis* marsh.

alternating horizontal layers of organic material and mineral material to a depth of at least 6 feet. This indicated the occurrence in the past of alternating periods of deposition of inorganic and organic material. This marsh was typical of numerous stream channels of the upland. Characteristics (Table III) are the high frequency of *Carex aquatilis, Hedysarum alpinum* var. *americanum, Saxifraga cernua, Arctagrostis latifolia, Stellaria laxmannii* and mosses.

Stand 64. *Carex aquatilis*-marsh

This marsh, 0.6 mile northwest of Umiat, was located in an old stream scar about 25 feet wide on the edge of a low terrace adjacent to the high terrace. To the east and west of the area sampled were small bodies of open water which marshes of this type were invading from all sides. The site was very wet and so level that the microrelief was insignificant. No surface drainage was possible. There was a uniformly distributed straw cover with a value of 3+ over the surface. This marsh is characterized by the high frequency of *Carex aquatilis* and mosses.

Discussion of Carex aquatilis-Marsh Type.—*Carex aquatilis* (Table III) with high frequency and moderately high cover, and *Eriophorum angustifolium, Salix fuscescens* var. *reducta* and *Caltha palustris* var. *arctica* with varying cover and frequency are present in the 3 stands. *Betula nana* ssp. *exilis* is present in Stands 64 and 67 which were in the floodplain marshes. There are more species of forbs in the upland marsh than in the 2 floodplain marshes. The moss cover is low in Stands 55 and 64 but moderately high in Stand 67 where approximately 50% of the moss cover consists of *Sphagnum* spp. the occurrence of which might have resulted from the larger area of standing water in this stand. Marsh types are widespread on the floodplain but only 2 stands were selected for study.

By the frequency-homogeneity test, Stands 64 and 67 are homogeneous with ratios of 1 to 0 and 3 to 1 respectively and Stand 55 is heterogeneous with a ratio of 2 to 2. The homogeneity-index of 100.0 for Stand 64 is unusual; however, only one species is concerned. The homogeneity-index of Stand 55 is higher than that of Stand 67, even though Stand 55 is heterogeneous by the frequency-homogeneity test.

DISCUSSION

The field methods were found to be especially applicable to aerial photographic interpretation studies of the Umiat area and would be equally applicable to similar areas. A greater volume of detailed phytosociologic data on plant communities of arctic, subarctic, alpine and subalpine areas is available for central European and Scandinavian areas than for comparable areas in North America. Use of the modified Hult-Sernander cover scale and the association table permits detailed comparison with data from these other areas. In addition, the sampling methods provided the detailed data required for correlation of the registration characteristics of the respective stands on aerial photographs.

Because of the nature of most communities of the Umiat area, *i.e.,* the many combinations of presence and abundance of dwarf shrub heath species and associates, the recognition and analysis of even closely related communities is essential to secure an understanding of the vegetation and to determine the manner in which certain combinations and variations register on the aerial photographs. These different combinations discernible on aerial photographs may be indicative of important environmental conditions. Life-forms of the area are restricted to a few kinds and these are usually intermixed in the dense vegetation. Therefore, on aerial photographs (images reduced 7,500 to 20,000 diameters) the physiognomic characteristics resulting from life-forms cannot serve as adequate criteria for the delimitation of communities in this region.

After considerable detailed field data had been obtained, it was suspected that due to the nature of the communities of the Umiat area, the frequency of selected species present in each community is one of the most important phytosociological characteristics. This is especially true since the cover of each species is class 1 in the majority of stands. The collection of additional field data and subsequent analysis of all data tend to confirm this observation. Several studies (Nordhagen 1928, 1943, Hanson 1953) indicate that usually in the tundra it is not common for all species to be present in cover class 1. For example, Hanson (1953) shows in several association tables that average cover ranges from 2 to 4 for 2 to 4 species per stand.

The frequency-homogeneity test and the homogeneity-index tend to show relationship to each other in the degree of homogeneity or heterogeneity. Homogeneous stands usually have the higher homogeneity-indices and the heterogeneous stands have the lower homogeneity-indices. However, absolute correlation of these values cannot be expected. Only in relatively few cases are the same number of species included in the compilation of each value. The frequency-homogeneity test is concerned only with those species with frequencies of 61 to 100%. The homogeneity-index includes all species of the floristic-characteristic-species-combination and even though some species may and do have frequencies equal to or less than 60%. Only in Stands 20 and 70, both in the Eriophorum Tussock-Dwarf Shurb Heath Subtype, are all the vascular species of the floristic-characteristic-species-combination present with frequencies greater than 60%. In the majority of cases, the frequency-homogeneity test includes the majority of species of the floristic-characteristic-species-combination so that close correlation of results by both indices results and is to be expected.

Analysis of both the homogeneity-index and the frequency-homogeneity test is of material assistance in the interpretation of aerial photographs. These indices show minute differences of homogeneity or heterogeneity of registration of the respective stands on the aerial photographs.

Two indices are computed for the comparison of the degree of relationship between stands. The coefficient of affinity, as a result of the relative ease of computation, is of assistance in the preliminary comparison and grouping of stands and in determining the pairs of stands for which the more sensitive Sörenson coefficient is to be computed. There is a tendency for the Sörenson coefficient to have a lower value than the coefficient of affinity. Both coefficients are of assistance, not only in indicating the degree of relationship between two stands, but also in determining the relative important of individual species and groups of species with respect to the degree of relationship between 2 stands.

The various indices are of material assistance in the preliminary analysis and grouping of stands into types. No single index or group of indices can be used as firm criteria for grouping into types and subtypes. Final grouping is based upon detailed analysis of association tables supplemented by reference to the various indices; thus the stands are grouped into 5 types and 6 substypes, as follows:

- Dwarf Shrub Heath Type
  - Eriophorum Tussock-Dwarf Shrub Heath-Subtype
  - *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtype.
  - Carex-Dwarf Shrub Heath Subtype
  - Grass-Dwarf Shrub Heath Subtype
- Frost-Scar Collective Type
  - *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype
  - Dwarf Shrub Heath Frost-Scar Subtype
- *Salix* Type
- *Alnus crispa* Type
- *Carex aquatilis*-Marsh Type

The Dwarf Shrub Heath Type is characterized by the greater number and higher frequencies of dwarf shrub heath species and associates. This is also generally the case with the Dwarf Shrub Heath Frost-Scar Subtype which is closely related to the Dwarf Shrub Heath Type. The dwarf shrub heath species and associates also occur in other types but here they are relatively less important. The Dwarf Shrub Heath Type is characterized by the similar occurrence of dwarf shrub heath species in all stands; it is subdivided into 4 subtypes on the basis of the relative frequencies of *Eriophorum, Carex,* and grass species, which is indicated diagrammatically below:

Eriophorum > *Carex* > grass
Eriophorum Tussock-Dwarf Shrub Heath Subtype

Eriophorum = *Carex* = grass
Eriophorum spissum-Carex lugens-Arctagrostis latifolia-Dwarf Shrub Heath Subtype

Carex > grass > *Eriophorum*
Carex-Dwarf Shrub Heath Subtype

Grass > *Carex* > *Eriophorum*
Grass-Dwarf Shrub Heath Subtype

It may be that these 4 subtypes represent phases of a cyclic succession within the Dwarf Shrub Heath Type.

The most important feature of the Frost-Scar Collective Type is the presence of bare frost scars surrounded by vegetation, usually in depressions of the microrelief. The phytosociologically distinct subtypes are the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype and the Dwarf Shrub Heath Frost-Scar Subtype. Causes for frost scars have been discussed in a recent paper by Hopkins and Sigafoos (1951).

The Salix Type is characterized by the high frequency, moderately high cover and height of *Salix* spp. The type may be successional, though long-enduring, in which case the other species present may indicate the successional trend toward a dwarf shrub heath type. In northwestern Alaska, similar *Salix* types cover extensive areas (Hanson 1953).

The *Alnus crispa* Type is characterized primarily by the high frequency and cover of *Alnus crispa* and secondarily by the relatively high frequency and moderate cover of *Salix* spp. The dense crown canopy of *Alnus crispa* and *Salix* spp. excludes a well-developed ground cover of other species. Alder communities have been described briefly by Porsild (1939) and Hanson (1951, 1953).

Characteristics of the *Carex aquatilis*-Marsh Type are the high frequency of *Carex aquatilis,* the very wet habitat, and the presence of few other species. Because of the very wet habitat, few other species are to be expected. However, since the type is successional yet long persisting, an analysis of more advanced stages would indicate the course of succession which would probably terminate with a dwarf shrub heath. This type or similar types are widespread in northern regions (Hanson 1951, 1953, Nordhagen 1943).

Some features of the more prominent species are discussed below.

Alnus crispa, besides being the dominant of a distinct type, is widespread within the other types. It does not occur in the Frost-Scar Collective Type, possibly because of the unstable environment, or in the *Carex aquatilis*-Marsh Type, because of the extremely wet habitat.

A total of 17 species and varieties of *Salix* occur in all the types; there is one distinct *Salix* Type. Sixteen species of *Salix* occur in the Dwarf Shrub Heath Type, 12 in the Eriophorum Tussock-Dwarf Shrub Heath, 12 in the Carex-Dwarf Shrub Heath, 6 in the Grass-Dwarf Shrub Heath, and 5 in the *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtypes. Five species are present in the Dwarf Shrub Heath Frost-Scar and 2 in the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtypes, 5 in the *Alnus crispa* Type and only 1 in the *Carex aquatilis*-Marsh Type. *Salix pulchra* is the most widespread, occurring in all types and subtypes except the *Carex aquatilis*-Marsh Type. There are 5 species and varieties which occur in only one type: *Salix alaxensis* in the Salix Type, *S. glauca* var. *acutifolia* and *S. glauca* var. *Aliceae* in the Carex Dwarf Shrub Heath Subtype, and *S. pulchra* var. *yukonensis* in the Eriophorum Tussock-Dwarf Shrub Heath Subtype. Generally, if the frequency of either *Alnus crispa* or a *Salix* spp. is high, then the frequency of the other is relatively low.

The dwarf shrub heath and associated species are especially important in the Dwarf Shrub Heath Type and the Dwarf Shrub Heath Frost-Scar Subtype. They are present with less importance in the other types and subtypes. *Betula nana* ssp. *exilis* is present in 8 types and subtypes. It is the only dwarf shrub species in the *Carex aquatilis*-Marsh Type, and is absent from the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype. *Arctostaphylos alpina, Ledum decumbens, Vaccinium uliginosum* and *V. vitis-idaea* occur in 7 types and subtypes. *Vaccinium oxycoccus* is present in only the Eriophorum Tussock-Dwarf Shrub Heath Subtype. *Dryas integrifolia* (var. *canescens*?) and *Rhododendron lapponicum* are present only in the Carex-Dwarf Shrub Heath, Grass-Dwarf Shrub Heath, and the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtypes. *Cassiope tetragona* is not present in the Salix, *Alnus crispa* and *Carex aquatilis*-Marsh Types, probably indicating a lack of tolerance for shading and excessive moisture.

Eriophorum spissum is the most common species of this genus. Its occurrence is most prominent in the Eriophorum Tussock-Dwarf Shrub Heath and the *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath Subtypes. It is not present with a cover rating in the Grass-Dwarf Shrub Heath and *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtypes, and the *Alnus crispa* and *Carex aquatilis*-Marsh Types. *Eriophorum vaginatum* replaces *E. spissum* in 1 stand of the Eriophorum Tussock-Dwarf Shrub Heath. *E. angustifolium* is present in the *Carex aquatilis*-Marsh Type.

Carex lugens has the greatest occurrence in almost all types and subtypes. It is not present in the *Dryas integrifolia* (var. *canescens*?) Frost-Scar Subtype and the *Alnus crispa* and *Carex aquatilis*-Marsh Types. Other species of *Carex* are also present in some of the types and subtypes. In 3 stands of the Eriophorum Tussock-Dwarf Shub Heath Subtype, *Carex consimilis* replaces *C. lugens* in importance and in 3 stands of the Carex-Dwarf Shrub Heath Subtype, *C. lugens* is replaced in importance by *C. scirpoidea, C. consimilis, C. vaginata* and *C. membranacea.*

Arctagrostis latifolia, usually sparse, has the most general occurrence of the grasses. It does not occur in the *Dryas integrifolia* (var. *canes-*

cens?) Frost-Scar Subtype and the *Carex aquatilis*-Marsh Type. *Hierochloe alpina* and *Poa arctica* are commonly associated with *Arctagrostis latifolia* in the types and subtypes.

Stellaria laxmannii is the only forb which is present in all types and subtypes. *Polygonum bistorta* ssp. *plumosum* and *Pyrola grandiflora* are also widespread in occurrence, each being present in 7 types and subtypes *Polygonum bistorta* ssp. *plumosum* is not present in the *Alnus crispa* and the *Carex aquatilis*-Marsh Types; *Pyrola grandiflora* is not present in the Dwarf Shrub Heath Frost-Scar Subtype and the *Carex aquatilis*-Marsh Type. *Lupinus arcticus* is present in 3 Dwarf Shrub Heath Subtypes but not in the Grass-Dwarf Shrub Heath Subtype; it is present in both Frost-Scar Subtypes but not in the remaining types. The greatest number of forb species occur in the Dwarf Shrub Heath Type and the *Dryas integrifolia* (var. *canescens?*) Frost-Scar Subtype.

Summary

1. The general aspect of the Umiat area, located between the Brooks Range and Barrow, Alaska, results from the presence of gently rolling hills with dense vegetation generally 6 to 12 inches high consisting of dwarf heath shrubs, dwarf birches and willow, intermingled herbaceous species and, in places, alders and willows from 3 to 8 feet high. The tall alders and willows occasionally form thickets, especially on slopes and on the flood-plain.

2. The environment of the Umiat area is rigorous, annual precipitation is very low, the winters are long and severe, and the summers are cool and short. No freeze-free season can be expected, and permanently frozen ground underlies the area at usually shallow depths.

3. Eighty stands of various plant communities were investigated during the summer of 1951 in the Umiat area of Alaska. Quadrat analysis and soil profile descriptions were made in each stand.

4. Aerial photographs were found to be useful in differentiating, delineating, and selecting stands for detailed analysis since differences were more readily detected on aerial photographs than on the ground.

5. Frequency is one of the most important phytosociological characteristics because the cover of each component species of a stand is usually low to an equal degree.

6. Association tables and phytosociological indices are useful in analyzing stands, in comparing stands, in determining relationships of stands and in evaluating the phytosociological importance of species.

7. The stands are grouped into 5 types. The most widespread type, the Dwarf Shrub Heath, is divided into 4 subtypes, Eriophorum Tussock-Dwarf Shrub Heath, *Eriophorum spissum-Carex lugens-Arctagrostis latifolia*-Dwarf Shrub Heath, Carex-Dwarf Shrub Heath and Grass-Dwarf Shrub Heath. The Frost-Scar Collective Type is divided into the *Dryas integrifolia* (var. *canescens?*) and the Dwarf Shrub Heath Subtypes. The other three types are the *Salix*, the *Alnus crispa* and the *Carex aquatilis*-Marsh Types. Microhabitats, and therefore the microcommunities which they determine, are characteristic of the first 2 types so that these types could be considered as mosaics of microcommunities. These types display a homogeneity which results from the uniformity of distribution of microcommunities within the stand.

8. The most important vascular species with regard to cover and frequency are *Alnus crispa, Arctostaphylos alpina, Betula nana* ssp. *exilis, Cassiope tetragona, Dryas integrifolia* (var. *canescens?*), *Empetrum nigrum, Ledum decumbens, Vaccinium uliginosum, V. vitis-idaea, Salix glauca, Carex aquatilis, C. lugens, Eriophorum spissum, Arctagrostis latifolia, Lupinus arcticus, Polygonum bistorta* ssp. *plumosum, Pyrola grandiflora* and *Stellaria laxmannii.*

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REGULATORY MECHANISMS OF HOUSE MOUSE POPULATIONS: SOCIAL BEHAVIOR AFFECTING LITTER SURVIVAL[1]

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This paper presents data on the social environment of house mice which accompanies crowding and which influences litter survival. Five aspects of the social environment are considered: aggressiveness, gregariousness, intermingling of sexes, nest destruction, and abnormal communal nesting.

Poor litter survival was found to be the major controlling mechanism of confined populations of wild house mice supplied with unlimited food (Southwick 1955). This poor survival resulted primarily from improper parental care: such behavioral traits as cannibalism, desertion, trampling or scattering of the young. No attempt is made in this paper to assess the relative importance of these specific behavioral traits. It was often impossible to disentangle them and assign only one as the actual cause of death. Some young, when found dead, were partially consumed, but others were intact or possessed only minor wounds, and could have died from a number of causes including being trampled, deserted, or bitten. Hence, the behavioral traits of cannibalism, desertion, trampling, etc. are all considered in this paper under the general heading of improper parental care.

Many workers have observed improper parental care to be an important mechanism of population control under crowded conditions (Alverdes 1935; Solomon 1949). It has been particularly noted in house mice (Brown 1953; Crew and Mirskaia 1931), Norway rats (Calhoun 1949), British voles (Chitty 1952; Ranson 1941), muskrats (Errington 1939), and rhesus monkeys (Carpenter 1942). Considerable challenge exists, therefore, to study the social environment in which improper parental care occurs.

I wish to thank Prof. John T. Emlen for frequent help throughout this study, and my wife, Heather, for assistance with the manuscript. The experimental populations of this study were housed on the arboretum of the University of Wisconsin. I am indebted to the arboretum committee and staff for providing these facilities.

METHODS

Six experimental populations of house mice were each confined in an uncovered pen six feet wide and 25 feet long. Each pen contained 48 nest boxes, 2 x 3 x 6 inches in dimensions, and an abundance of food, water, and nesting material. The pens were lined with sheets of galvanized iron 24 inches high which effectively contained the mice.

On November 22, 1950, four pairs of wild house mice, trapped from natural infestations on the University of Wisconsin campus and selected as healthy young adults, were released into each of the six pens. In three of the pens, A, C and E, the nest boxes were crowded at one end and the food and water facilities were placed in large containers at the opposite end. In the other three pens, B, D and F, the nest boxes were widely dispersed around the two long sides of the pens and the food and water were placed in 24 bowls down the center of the pen. Photographs and a floor plan of the pens are given in a previous paper (Southwick 1955). Each pen received the same amount of food and nesting space; only the dispersion differed.

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[1] Contribution from the Department of Zoology, University of Wisconsin. The work described in this report was supported by funds from the National Institutes of Health and the Wisconsin Alumni Research Foundation.

The populations were permitted to grow without unnecessary disturbance for two years. Every two weeks the nest boxes were inspected for litters and the birth date of all litters, dead or alive, was estimated by age criteria given in Snell (1941). Bacterial cultures from freshly dead nestlings were occasionally made by Dr. Geoffrey Lord, then of the Department of Veterinary Science, University of Wisconsin. Every four weeks all the mice were caught, weighed, examined externally for health and breeding condition, and their nest box location was recorded. All individuals were marked (by toe clipping) when approximately two weeks of age. These census checks upset the routine of the mice for one to several hours, but no adverse effect on litters or adults was noted. These were basically the same procedures used by Strecker and Emlen (1953).

Nesting material in the form of shredded paper and cotton waste was added *ad lib.* until continued additions were not utilized by the mice. This generally occurred about the 18th month of the study. Nests were classified as *platform,* if only a flat layer of nesting material existed; *bowl,* if a definite hollow was present; or *covered,* if the nest cavity was completely surrounded by nesting material. This follows the convention of Brown (1953).

Behavior observations were made with a specific effort to index the amount of aggressive activity occurring within the populations. Observations were made in the evening, from two to four hours after sunset, and the observing was done from a high chair which provided a good view of the pens. Lights were turned on in the afternoon, so that the animals were little disturbed by the entrance and presence of the observer in the evening. For each pen, the number of fights or aggressive interactions were recorded. The descriptions of Scott and Fredericson (1951) were utilized as a guide for distinguishing true fighting behavior from sexual behavior.

The barracks housing the pens was centrally heated by a coal furnace. This proved inadequate until December of the first winter, when an oil burner was installed to provide constantly favorable conditions.

AGGRESSIVENESS

One of the obvious forms of social disturbance affecting parental care was the tendency to fight. Counts of the number of aggressive encounters indicated that aggressive activity within each pen increased as the number of mice in that pen increased (Fig. 1, Table I). In this sense, the amount of aggressive activity within any one population might be considered density-dependent. Yet fighting varied greatly between populations irrespective of density. Apparently, elements of individual behavior and social structure were major determinants of these population differences, forming the foundations upon which

TABLE I. *Relationships between population size and intensity of aggressive activity*

Month	Hours of observation per Pen	Pens											
		A		B		C		D		E		F	
		Pop.[1]	A.I.[2]	Pop.	A.I.	Pop.	A.I.	Pop.	A.I.	Pop.	A.I.	Pop.	A.I.
8/51.......	23	14	0.08	58	0.31	7	0.07	18	0.04	17	0.46	16	0.08
9/51.......	24	32	0.07	57	0.22	16	0.12	15	0.15	15	1.25	16	0.09
10/51.......	7	36	0.03	57	0.30	28	0.06	14	0.04	13	0.31	14	0.26
11/51.......	5	32	0.03	53	0.32	24	0.01	13	0.02	12	0.10	14	0.14
12/51.......	6	35	0.19	49	0.27	23	0.01	13	0.02	10	0.16	13	0.15
1/52.......	15	32	0.43	46	0.24	28	0.08	13	0.01	9	0.02	11	0.06
2/52.......	10	31	0.37	42	0.42	45	0.09	13	0.18	8	0.00	9	0.19
3/52.......	10	61	0.37	68	0.61	48	0.48	28	0.07	7	0.03	19	0.14
4/52.......	10	91	0.76	63	1.05	63	1.06	34	0.35	7	0.04	23	0.32
5/52.......	6	98	0.66	73	0.97	90	1.02	64	0.60	6	0.03	26	0.27
6/52.......	10	118	0.79	74	1.12	100	1.31	109	0.60	5	0.04	36	0.14
7/52.......	8	130	0.75	77	1.02	113	1.18	138	0.68	5	0.18	52	0.52
8/52.......	10	131	0.98	75	1.14	114	1.15	137	1.00	13	0.18	46	1.07
9/52.......	10	131	0.99	75	1.06	127	1.21	131	1.00	20	0.42	59	0.89
10/52.......	2	128	0.95	67	0.82	120	1.18	134	0.86	25	0.50	53	1.26

[1] Pop. = number of postweaned mice in population.
[2] A. I. = aggressive interactions per hour per postweaned mouse.

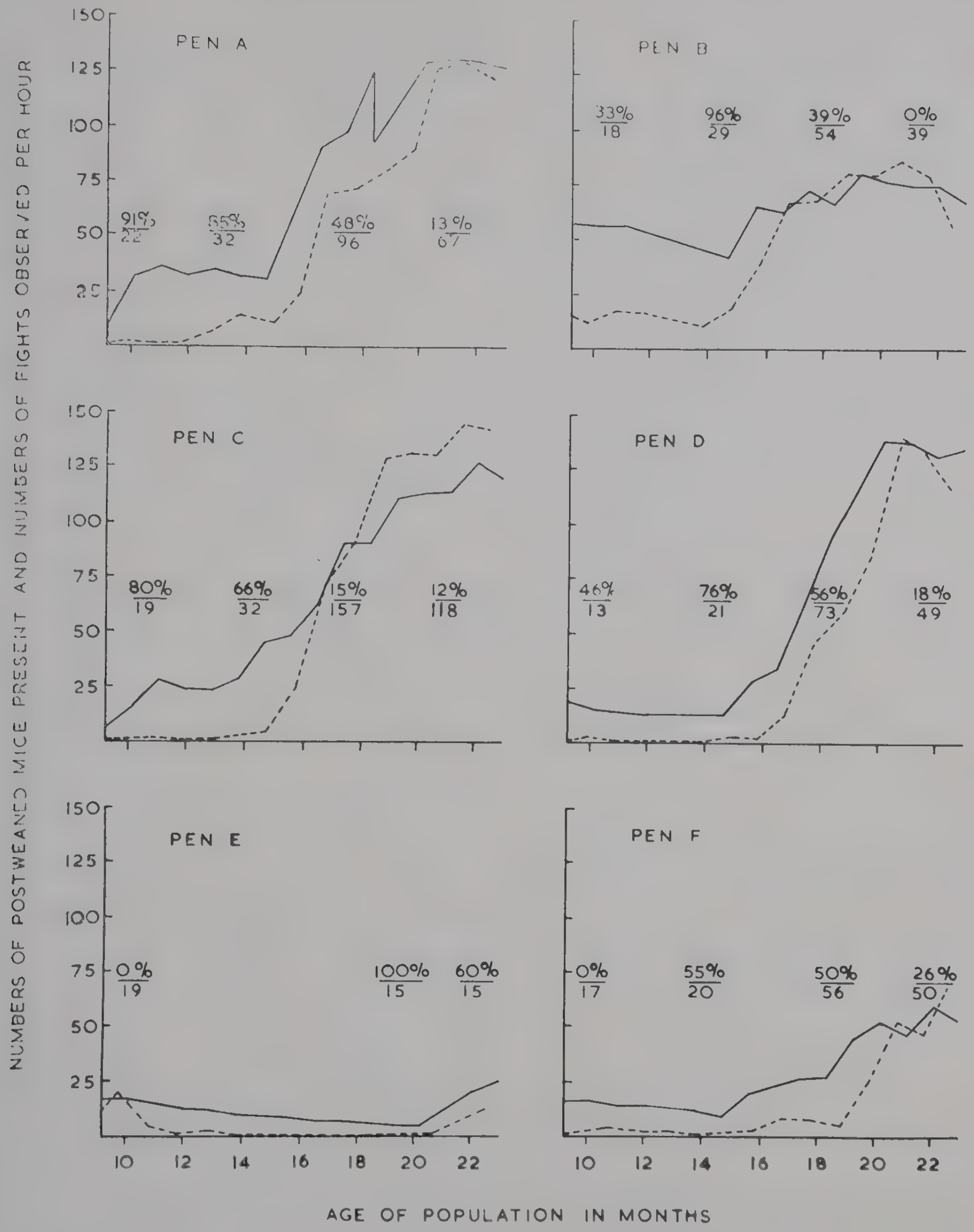

FIG. 1. Relationships of population growth and litter survival to amount of aggressive activity observed.

——— Numbers of postweaned mice

-------- Numbers of fights observed per hour

$\frac{91\%}{22}$ $\frac{\text{Per cent survival to weaning of young born in a two-month period}}{\text{Number of young born in a two-month period}}$

density-dependent aggressive activity could operate.

In general, when the populations built up to the point at which fighting occurred at the observed rate of about one aggressive encounter per hour per mouse, litter survival had fallen so low that population growth ceased or was slowed (Fig. 1). This point was independent of density between pens. For example, Pen E revealed excessive litter mortality which stopped population growth in the summer of 1951 at a level of 17 mice and 20 aggressive encounters per hour. Pens A and C did not reveal this excessive litter mortality until they had attained levels of approximately 130 mice and 130 to 140 aggressive encounters per hour. Pens B, D and F were also ultimately controlled by litter mortality at varying densities but similar indices of aggressive activity.

Although this generalization holds for the ultimate levels attained by the populations, a direct relationship between the amount of aggressive activity and litter survival did not always exist in the earlier stages of population growth. September, 1951, was an interesting period with two populations increasing and four remaining stationary or declining. The two increasing populations, A and C, revealed low indices of aggression (Table I) and good litter survival (94% of 18 young). Of the four stationary or declining populations, all of which revealed 100% litter mortality, only Pen E displayed an intense amount of aggressive activity. These data suggest that low litter survival may accompany and possibly result from intense aggressive activity, but also that litter survival is obviously influenced by other aspects of social behavior.

The meaning of these generalizations on the relation of aggressiveness to litter survival can best be studied by examining the situations in which fighting occurs and the effects of aggressive activity on individuals.

Aggressive interactions apparently function to determine and maintain a social hierarchy within the group (Brown 1953; Collias 1944; Uhrich 1938). Both laboratory and wild house mice frequently display a monoarchistic type of social order in which one dominant male tends to inhibit aggression between all other subordinate males in the group (Brown 1953; Scott and Fredericson 1951; Uhrich 1938). A well-stabilized hierarchy, therefore, may have a relatively low level of fighting, but when shifts or disruptions in the social structure occur, as through the maturation of new individuals, more active fighting takes place (Brown 1953). My observations agree with these concepts. The social structures in the rapidly growing populations of this study were constantly disrupted by the sexual maturations of young mice and the deaths of old mice.

Where unusually aggressive individuals are present, a situation may arise in which the whole population is disrupted by social disturbances emanating from one or a few individuals. Calhoun (1949) noted this in a confined population of Norway rats, and I observed it in Pen E where an adult male, which happened to be albino, became particularly aggressive during the summer and fall of 1951. He would frequently chase other mice from the food tray, and often provoked a fight for no apparent reason. He was the initiator of many "chain reaction" fights. At the height of his career in September, 1951, 20 fights per hour were counted in the pen. In late September, however, this male was noted to be losing his dominant position, and in one or two fights he was defeated. On October 4, he was found dead, apparently having been killed in a fight. An abrupt decline in aggressive activity in the population was noted after his death, and for October an average of only 4.4 fights per hour was tallied.

The aggressive tendencies of mice may be influenced by the genetic makeup of the individual (Scott 1942), its hormonal balance (Beeman 1947), its infantile experience (Fredericson 1951; Kahn 1954), and its learning in later life (Uhrich 1940). Scott and Fredericson (1951) presented evidence that experience and training are among the most important factors affecting the fighting tendencies of a mouse.

In my populations, both males and females were seen to initiate fights, but males were by far the most active aggressors. Uhrich (1938) and Brown (1953) found fighting in house mice to be most prevalent among the males, but Brown (1953) and Crowcroft (1954) have observed that females may become notably aggressive shortly before or after parturition.

In most of the fights I observed, the mice did not seem to be fighting over the possession of any goal object. Two mice would suddenly meet and fight, and the provoking element could seldom be discerned. Scott and Fredericson (1951) have termed this "noncompetitive fighting" and noted in rats and mice that it is more violent and injurious than "competitive fighting" (fighting over the possession of a goal object). Their studies indicated that the factors initiating noncompetitive fights are sudden movements, noise, pain, restraint, and the male hormone. Thus, noncompetitive fighting is more prevalent among males and it is a self-catalytic phenomenon; that is, one fight by producing pain, noise and sudden motion, stimulates additional fights. Calhoun (in Scott and Fredericson 1951) suggested that in noncompetitive fighting, rats and mice fight for undisturbed occupation of living space, rather than for any particular area. My observations agree with this idea. An aggressive mouse seemed to maintain a small area about him and would attack other mice coming in too close. Often this area was only two or three inches in radius; in other cases, such as the highly aggressive male in Pen E, it extended two or three feet. This area was not consistently defended, and could not be designated as a territory.

It is understandable, from these observations, why aggressive activity may show density-dependence within a population, yet reveal density-independence between populations.

Some competitive fighting was seen in my populations. Fights which seemed related to the possession of a food particle were rare but would occasionally arise at the feeding area. A more common type of fighting, which appeared to be competitive, occurred in the next boxes. Frequently, a fight would take place within a nest box and, amid squeaks and rattling, a mouse would emerge being pursued by another mouse. Scott and Fredericson (1951) mentioned the possibility that mice may fight over nests, and Brown (1953) recorded definite observations of nest defense by the female.

Although fighting in the nest boxes gave the appearance of competition for nest sites, there were always empty nest boxes, even at the peak of the populations. It is perhaps more likely, therefore, that real competition for nest boxes did not exist, and that aggression occurring within the boxes was largely another manifestation of noncompetitive antagonism.

The mechanism by which intense aggressive activity has a detrimental influence on litter survival might be at least threefold. Primarily, fighting in the nest boxes could cause death of the nestlings by trampling, scattering or wounding. Secondly, severe fighting might produce phychological and physiological stress altering the endocrine balance of the adults (Christian 1950; Clarke 1953), and thus altering normal parental behavior (Wiesner and Sheard 1933). Thirdly, fighting in and about the nest boxes would create an unfavorable and frightening social environment to which older nestlings (12 to 25 days of age) would be particularly sensitive in the development of their adult behavior patterns (Williams and Scott 1953).

GREGARIOUSNESS

The gregarious tendency of mice is a second major aspect of social behavior affecting the survival of litters. House mice are well known to huddle together in very close confines even when ample room is available (Strecker and Emlen 1953; Vogel 1951). This grouping occurs in either warm or cold temperatures, and it is accentuated at high population densities. In February, March and April, at low population densities, nest boxes containing young had an average of 2.8 adults present when the litter was found; while in August, September and October when the populations were high, nest boxes containing young held an average of 5.8 adults, although plenty of empty boxes were present.

Survival data (Table II) indicate a higher survival in nest boxes with one or two adults than in boxes with 3 or more adults. However, the sample is biased since more litters with 3 or more adults present occurred after the population peaks (July through October) and therefore the poor survival might actually be due to some factor other than the number of adults present. This possible bias was eliminated by excluding the data from July to November, and examining only those litters born before the population peaks (Table III).

Under this procedure, the figures of average survival become higher in all classes, as would be expected, yet the differences still remain. The survival of litters which were found with only one

TABLE II. *Survival of litters related to number of adults present when litter was found. Total available data. Values of Chi-square that are significant to the .05 and .01 levels are shown by one and two asterisks, respectively*

Number of adults present	Number of litters	Number of young	Number of young surviving	Percent survival	Chi-square[1]
1........	55	248	144	58	7.895**
2........	72	376	216	57	10.688**
3 or 4....	52	253	93	37	4.560*
5 or more.	57	267	72	27	20.492**

[1] Expected survival if all litters were drawn from a population exhibiting homogeneous litter survival=525/1144=45.9%.

TABLE III. *Survival of litters related to number of adults present when litter was found. Data from July to November, 1952, are excluded*

Number of adults present	Number of litters	Number of young	Number of young surviving	Percent survival	Chi-square[1]
1........	46	213	130	61	2.557
2........	48	249	159	64	5.528*
3 or 4....	34	170	79	46	1.344
5 or more.	33	162	54	33	11.907**

[1] Expected survival if all litters were drawn from a population exhibiting homogeneous litter survival=422/794=53.1%.

or two adults in attendance was 63%, significantly higher than the 46% survival of litters in which three or four adults were present, and the 33% survival of litters with five or more adults present (Table III).

Such an analysis is limited, of course, since only one observation of the adults in attendance with a litter was available, and the previous or subsequent history was unknown. These data, however, are in close agreement with observations by Brown (1953) who noted in dense populations of house mice that nesting females were no longer able to isolate themselves from disturbing activities of other mice, and successful weaning of litters decreased as the disturbance to parturient females by other mice increased.

INTERMINGLING OF SEXES

The intermingling of sexes at the nest site is a third aspect of social behavior apparently influencing litter survival. Data presented in Table IV suggest that the presence of one or more adult males in a nest box had a detrimental effect on litter survival. Survival of 107 litters with one or more adult males attending was between 19% and 31%, whereas survival of 129 litters attended by females only averaged 59%. The number of adult males in attendance with a litter made little difference on its survival; the presence of one male was as harmful as the presence of several when the data are grouped as in Table IV.

This conclusion is in disagreement with the intensive observations on this subject by Brown (1953). Brown directly observed that additional adult females provided a greater disturbance upon a nesting female than did adult males. He noted in the nest boxes that adult males displayed a general disinterest in the litter, even trending toward avoidance, whereas other adult females frequently displayed excited interest in the litter, ranging as far as partial usurping of the nest. My data agree with Brown's that crowding by adult females significantly reduced litter success (Table IV), but correlating the evidence on the specific influence of males requires further study.

TABLE IV. *Survival of litters related to number and sex of adults present when litter was found. Total data.*

Number of adults present	Number of litters	Number of young	Number of young surviving	Percent survival	Chi-square[1]
I. Only adult females present					
1........	45	205	136	66	18.766**
2........	52	281	196	70	34.798**
3 or 4....	25	143	60	42	0.545
5 or more.	7	42	3	7	13.474**
II. Adult males or adult males and females present					
1........	10	43	8	19	7.000**
2........	20	95	20	21	13.091**
3 or 4....	27	110	33	30	5.780*
5 or more.	50	225	69	31	11.223**

[1] Expected survival if all litters were drawn from a population exhibiting homogeneous litter survival = 525/1144 = 45.9%.

It is not an uncommon observation that adult males of various mammal groups may exhibit an antagonism toward breeding females and their young, an antagonism that can result in juvenile mortality, especially under crowded conditions (Allen 1943; Alverdes 1935; Carpenter 1942; Darling 1937; *et al.*). Although Brown (1953) reported no evidence of such antagonism in his house mouse populations, he did note that nesting females normally excluded males from their nests except under crowded conditions in which the females' nest defense was frequently broken and males entered the nest site.

Regarding actual consumption of the young, Brown (1953) found no evidence that males were involved in actual cannibalism. On two separate occasions, I saw males carrying young "pinkies" out of nests and chewing on them. Ranson (1941) recorded for the vole, *Microtus agrestis,* that either males or females may engage in cannibalism.

Three possible explanations exist for the effect of adult males on litter survival as seen in this study: (a) the males may kill the young directly, (b) the males may incite, by their mere presence, unfavorable female behavior toward the young, or (c) the relationship between poor litter survival and the presence of adult males is a nonsense correlation based on the possibility that males are found more commonly in poorer nests and that the poor nest site is actually the primary cause of poor litter survival. All may contribute; the present data do not provide the complete explanation.

NEST DESTRUCTION

In the early stages of this study, it became clear that the condition of the nest had an important influence on litter survival. Nest condition, in turn, was obviously affected by the social behavior of the population. As the populations increased throughout the spring of 1952, there was a decline in the number of well-built nests (Table V). This occurred even though abundant nesting material was supplied at all times until no more was utilized by the population (generally around June, 1952, in most populations). Apparently fewer females could maintain good nests in the presence of increased populations. Most of the nests would become trampled and matted into flat

TABLE V. *Percentages of forty-eight nest boxes in each population which contained good nests*[1]

Date	Pens					
	A	B	C	D	E	F
June to Sept., 1951	44	43	42	36	26	54
Feb. to Mar., 1952	10	24	5	28	42	58
May to Aug., 1952	0	4	1	7	46	17

[1] A "good" nest refers to any nest with a definite bowl-shaped nest cavity

TABLE VI. *Survival of litters related to type of nest and adult attendance*

Type of nest	Number of litters	Number of young	Number of young surviving	Percent survival	Chi-square[1]
I. Favorable adult attendance. Only one or two adult females present.					
No nest	3	18	0	0	12.000**
Platform	46	226	133	59	2.863
Bowl	24	123	77	63	0.583
Covered	10	43	37	86	2.207
II. Unfavorable adult attendance. At least one male and/or three or more females present.					
No nest	6	24	0	0	7.000**
Platform	64	341	63	18	7.290**
Bowl	9	44	25	57	11.076**
Covered	1	4	4	100	9.000**

[1] Expected survival ratio for favorable adult attendance = 332/486 = 68.3%. Expected survival ratio for unfavorable adult attendance = 193/658 = 29.3%.

platforms by the presence and activity of many mice.

Brown (1953) also noted that the nest condition was largely due to the amount of activity in the nest area by other mice. Under ideal conditions, with no interference, the pregnant females in Brown's study built deep nests. But under crowded conditions, a female building a nest would often be joined by other mice who were stimulated to "help" her. Some mice would remove one side of a nest to build up another side. Both males and females would often crowd into the nest under construction and trample a good bowl-shaped nest into a flat platform.

Brown (1953) classified nests into four types: no nest, platform nest, bowl nest, or covered nest. He recorded the percentage of litters with at least one young weaned as follows: 0.0% for 57 platform nests, 31.0% for 29 bowl nests, and 82% for 17 covered nests.

Similar data from the present study show higher survival percentages, but the basic relationships hold. Table VI tabulates litter survival according to nest condition and also according to the type of adult attendance, favorable or unfavorable. By favorable is meant only one or two adult females present with a litter; by unfavorable is meant one or more males, and/or several females (based on the preceding section).

It is noted that covered nests produced high litter survival (ca. 90%) regardless of adult attendance. Bowl nests produced moderately good survival (ca. 60%) regardless of adult attendance. Platform nests resulted in good survival (59%) if only one or two adult females were present, but in poor survival (18%) if unfavorable adults were in attendance. All litters born in boxes without nests suffered complete mortality.

ABNORMAL COMMUNAL NESTING

Communal nesting refers to the aggregation of two or more parturient females and their litters in a single nest site. Nests containing two or three litters of different ages occurred frequently in the populations of this study, and the survival of such litters compared favorably with that of solitary litters. Similar communal nests of house mice have been reported by Crowcroft (1954), Orr (1944), Strecker and Emlen (1953) and Vogel (1951). It is well documented, therefore, that communal nesting is a frequent and natural phenomenon in house mice.

Communal nesting reached abnormal levels in some populations of this study, however, as high density levels were attained. Under crowded conditions, communal nests were found containing five or more litters, and under these circumstances excessive mortality occurred. The most extreme case occurred in Pen C on July 28, 1952, when 58 young, all one to three days of age, were found in one nest box. None of these young survived past the fourth day. They were found in the presence of three adult females, which obviously could not have given birth to so many young. The other females contributing to this tremendous number of young had apparently deserted. Three other instances of this behavior were observed, and of 140 young born into such crowded circumstances, only 18 (13%) survived to weaning.

In communal nests containing litters of different ages, the litter which was born first frequently displayed the highest survival. Thus, of seven communal nests containing two litters of different ages, 36 out of 42 young of the first born litters survived (86%), while only 5 out of 33 young of the second born litters survived (15%). In Pen F, in a communal nest containing four distinct litters, the first two litters which were born had high survival (87%), the third litter born had low survival (33%), and the fourth litter of seven young failed to survive at all.

SUMMARY

The preceding sections have considered five aspects of social behavior associated with crowding and influencing litter survival; namely, aggressiveness, gregariousness, intermingling of sexes, nest destruction, and abnormal communal nesting. All of these factors increased in intensity with crowding and all of them apparently had a detrimental effect on litter survival. These factors interacted in such a way as to make it impossible to disentangle them and evaluate their relative importance in individual situations.

The amount of aggressive activity within each population increased as the density within that population increased, but different populations displayed widely variant aggressive tendencies. When the observed intensity of fighting reached approximately one fight per hour per mouse in each pen, litter mortality became excessive and population growth was greatly impaired.

As the populations increased, the number of adults attending litters was found to be higher and this was often accompanied by lowered litter survival. The presence of adult males with young litters was particularly associated with low litter survival.

The number of bowl and covered nests declined as the populations expanded despite plentiful nesting material. Mutual disturbances of the adult mice at high population densities prevented the maintenance of good nests.

Litter survival in bowl-shaped nests or covered nests was high (60% to 90%) regardless of the number or sex of adults present. Platform nests revealed good litter survival (59%) if only one or two adult females were present, but if several females or one male were present, litter survival in platform nests was low (18%). Zero survival occurred in 42 young born in boxes with no nests.

Communal nesting, which is a frequent and natural occurrence in house-mouse populations, assumed abnormal aspects in high density populations. In one instance, 58 young, all one to three days of age, were found in one nest. None of these survived.

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THE INTERRELATIONS OF LITTLELEAF, SITE INDEX, SOIL, AND GROUND COVER IN PIEDMONT SHORTLEAF PINE STANDS[1]

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The shortleaf pine forest type area increased 5.0 per cent, or from 2.0 to 2.1 million acres from 1936 to 1947. This increase was due chiefly to the reversion of a large acreage of agricultural land to forests. Much of this agricultural land was abandoned because it had deteriorated to such an extent that it no longer was profitable for farming. The severity of soil changes induced by cultivation under poor management practices has been studied by Hoover (1949). He showed that the non-capillary storage capacity of water in the top 2 feet of an uncultivated Vance forest soil was 4.05 inches, while in a similar soil cultivated and then abandoned 35 years ago and now supporting shortleaf pine, the non-capillary storage capacity was only 1.21 inches for the same depth. Similarly, in the surface soil the water percolation rate was twice as great in the uncultivated forest soil as in the abandoned field soil. In the subsoil, the rate was 60 times greater in the forest than in the old-field soil.

In 1949-1950, a soils-littleleaf survey was made in certain Piedmont counties of South Carolina and Georgia. This survey had several objectives: (1) to determine the relationship between littleleaf and soils on a wide area, (2) to evaluate specific soil factors associated with the incidence of littleleaf, and (3) to ascertain the occurrence of the fungus *Phytophthora cinnamomi* Rands in relation to littleleaf incidence and soil factors. Much of the information pertaining directly to littleleaf has been published by Campbell and Copeland (1954). Therefore, the object of this report is to summarize the soil conditions of South Carolina Piedmont shortleaf pine stands in relation to littleleaf and site index.

METHODS

The soils-littleleaf survey was planned to cover the counties within the shortleaf pine type. Disease conditions encountered ranged from healthy to severely diseased stands on many different soils. The number of one-quarter-acre plots sampled per county varied from 5 to 12 because of stand conditions and the proportion of forested lands. Representative plots in 30- to 65-year-old even-aged second-growth shortleaf pine stands were selected according to certain predetermined plot requirements. These were: (1) plots must be separated by at least 2 miles, (2) stands must be at least 30 years old, with a minimum stocking of 80 shortleaf pines 6 inches d.b.h. or larger per acre, and (3) plots must not be located in recently burned, pastured, or logged areas.

Stand tallies showing the composition and density were made by 2-inch diameter classes for all trees beginning with the 6-inch diameter class. Age and height of at least 5 dominant healthy shortleaf pine trees per plot were obtained and the site index at age 50 was determined from site index curves for second-growth southern pines published by the U. S. Department of Agriculture, Forest Service (1929).

Soil series and types upon which the plots were located were identified and the aspect and topographic position determined. The degree of erosion and rates of surface and internal drainage were determined in accordance with standards established by the Division of Soil Survey, U. S. Department of Agriculture (1951). Composite soil samples were collected by horizons from all plots for subsequent laboratory analyses.

Twenty-four soil samples from each plot were taken to a depth of 4 inches and were assayed by the apple technique described by Campbell (1949) to determine the abundance of the fungus *Phytophthora cinnamomi*. Litter samples were taken to determine the amount of litter on each plot. Understory and ground cover composition and density were also recorded.

LITTLELEAF, SITE INDEX, SOIL SERIES, AND PHYTOPHTHORA CINNAMOMI

Table I shows by counties the number of plots sampled, the per cent of littleleaf trees, the average site index, and the average per cent of soil samples from which *Phytophthora cinnamomi* was isolated. Order of arrangement is from the lowest to the highest average incidence of littleleaf. Although light littleleaf was observed in some cutover stands, Saluda County is shown as having zero littleleaf, because in adhering to the plot requirements relative to stocking, no plots sampled contained any diseased trees. The mean percent-

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[1] Grateful acknowledgment is made to the Champion Paper and Fibre Company for invaluable assistance rendered in connection with the field work of this survey. All fungus isolations were made by Dr. W. A. Campbell, Southeastern Forest Experiment Station, Athens, Ga.

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TABLE I. *A summary of the survey data on littleleaf, site index, and recovery of* Phytophthora cinnamomi, *arranged by counties*

County	Plots (number)	Little-leaf trees (per cent)	Average site index (feet)	Soil samples from which *P. cinnamomi* was isolated (per cent)
Saluda	7	0	71	26
Greenville	10	4	68	28
Oconee	10	4	64	22
Greenwood	7	6	64	17
Pickens	6	6	63	33
Anderson	9	7	54	12
York	12	8	65	31
Newberry	6	8	66	17
McCormick	5	10	61	16
Chester	7	13	49	17
Spartanburg	11	16	59	24
Union	10	16	58	31
Laurens	12	16	58	21
Lancaster	10	17	60	30
Abbeville	9	21	58	18
Elbert (Ga.)	5	22	60	13
Cherokee	10	23	58	36
Fairfield	12	29	55	25

tage of littleleaf-diseased trees determined by this survey for all counties is 12.6.

The counties survey may be divided into four groups according to the per cent of trees affected by littleleaf: (1) light littleleaf, with less than 5 per cent, (2) moderate littleleaf, with from 5 to 10 per cent, (3) severe littleleaf, with from 11 to 20 per cent, and (4) very severe littleleaf, where more than 20 per cent of the trees are diseased. This arrangement, shown in Figure 1, agrees closely with prior reports on littleleaf severity for many counties, as reported by Hepting and Cruikshank (1950).

The relationship between site index and littleleaf already reported by Copeland (1954) is confirmed by the data in Table I, which show that littleleaf is not severe in those counties having a generally high site index.

Recovery of *Phytophthora cinnamomi* from soils in the many counties is highly variable. There is no direct relationship between the recovery of this fungus from soil samples collected during this study and the incidence of littleleaf. This is understandable since it is known that *P. cinnamomi* is quite widespread in southeastern soils according to Campbell (1949), but variations in soil moisture and soil texture make it difficult to get quantitative estimates from the isolation work. Heavy-textured moist soils favor the isolation of this fungus much more than do light-textured dry

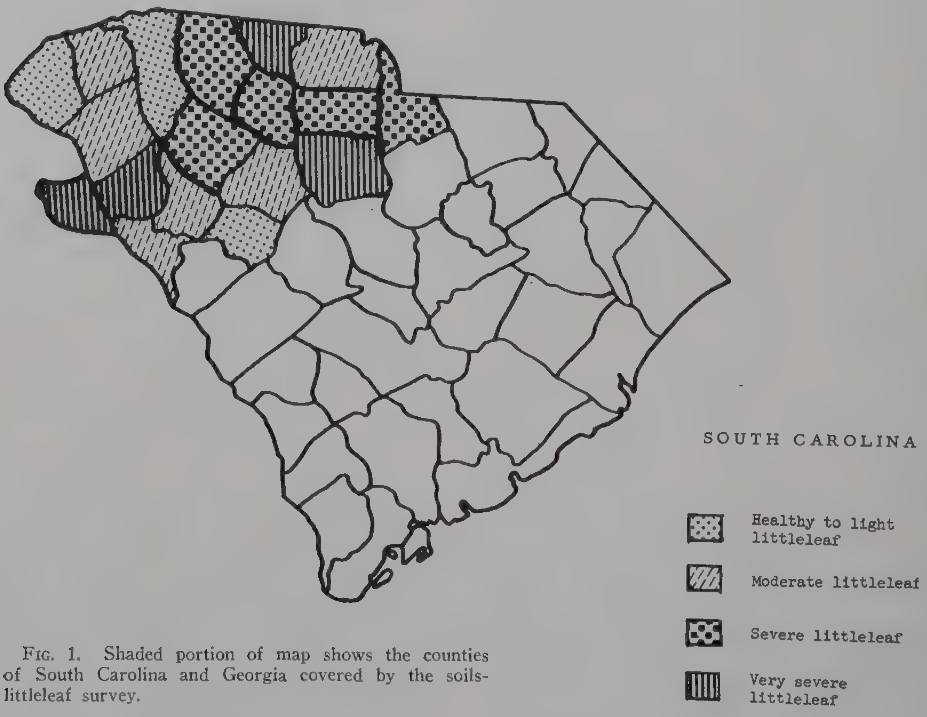

FIG. 1. Shaded portion of map shows the counties of South Carolina and Georgia covered by the soils-littleleaf survey.

soils. Generally, the fungus can be isolated from about one in every four soil samples.

Site index as used throughout this report represents height growth adjusted to 50 years of age. The site index of 85 per cent of the 158 plots ranged from 50 to 70 feet, and the mean site index for the total number of plots was 60.3 ± 0.49 feet. This mean may be slightly higher than the general average in the Piedmont because sample plots were not established in the very poorly stocked stands usually associated with a low site index.

The distribution of plots, average site index, average per cent of littleleaf trees, and average recovery of *Phytophthora cinnamomi* by soil series, grouped according to parent material, are shown in Table II. These data show that certain soils such as Cecil, Georgeville, and Davidson consistently support stands with high site indices. Soils such as Orange, Manteo, Wilkes, and Louisa support stands with lower site indices. Littleleaf incidence is generally also light on the former soils but much more severe on the latter soils. *P. cinnamomi* shows no definite trend by soil series.

An examination of the data also shows that the recovery of *Phytophthora cinnamomi* is considerably lower on sandy textured soils such as Appling, Durham, and Vance than on heavy textured or moist soils such as Cataula, Helena, and Mecklenburg. On the other hand, some soils having an abundance of *P. cinnamomi* but possessing excellent internal drainage such as Cecil, Almanance, Nason, and Georgeville support shortleaf stands that suffer little from attacks by the fungus. Explanations for this are proposed by Campbell and Copeland (1954).

Proper identification of soil series can aid materially in estimating the potential littleleaf hazard and site quality of an area that might be under consideration. However, past land management may exert a strong modifying influence on erosion and internal drainage, and soil series names alone can only be relied upon to indicate roughly what might be expected under normal conditions.

TABLE II. *Site indices, per cent of littleleaf trees, and* Phytophthora cinnamomi *isolations from plots located on various soil series arranged according to parent material groups*

Soil parent material	Soil series	Plots (number)	Mean site index (feet)	Standard error (feet)	Littleleaf trees (per cent)	Soil samples from which *P. cinnamomi* was isolated (per cent)
Granites, gneisses, and schists	Cecil	27	64	1.4	4	26
	Appling	11	55	2.2	13	17
	Durham	4	64	4.3	1	16
Porphyritic granite with large feldspar crystals	Lockhart	4	56	5.6	4	28
Aplitic granite or gneisses and basic rocks	Cataula	6	58	4.1	20	31
	Vance	22	58	1.8	23	20
Laminated slates (Carolina slates)	Georgeville	14	66	1.9	3	19
	Herndon	3	57	1.7	33	26
	Alamance	5	62	3.4	2	33
	Orange	2	50	5.0	22	27
Fine-grained serecitic schists	Manteo	2	55	—	37	38
	Tatum	2	60	—	32	52
	Nason	1	65	—	4	46
Basic rocks: idiorites, diabase, gabbro, and hornblende schists	Davidson	2	65	—	5	8
	Mecklenburg	13	59	1.9	22	27
Basic rocks intermixed with granites, gneisses, or schists	Wilkes	1	55	—	46	29
	Lloyd	9	61	4.3	9	20
	Helena	3	67	11.7	16	40
Quartz mica schists, mica schists, and garnetiferous schists	Madison	23	60	1.8	12	23
	Louisa	1	50	—	10	21
Mica schists	Fannin	1	70	—	0	25
Alluvium	Wickham	1	65	—	49	33
Not identified	Not identified	1	40	—	56	13

ASPECT AND SITE INDEX

The lowest mean site index (55.4 ± 1.1 feet) occurred on northeastern slopes, while the highest mean site index (63.2 ± 2.2 feet) was on northwestern slopes. Differences between the low mean site index on northeastern slopes and higher site indices on NW, SE, S, and SW slopes are significant at the 1 per cent level. Three aspects, NW, S, and SW, having significantly higher site indices, also had the lowest average per cent slope ranging from 8.4 to 10.1 per cent. The combination of steep slopes and the warmer aspects make for drier sites less favorable for maximum growth. No significant relationship was found between littleleaf incidence and aspect.

IMBIBITIONAL WATER VALUES AND SITE INDEX

The capacity of a soil to imbibe water may be taken as an indication of the amount of swelling and shrinking that may occur in soils, and this directly influences aeration and water movement. Soil characteristics, especially the amount and nature of the clay fraction influence the imbibing ability of soils. Imbitional water values were determined on soil samples collected from all plots essentially as outlined by Coile (1948), who has shown that these values of the B horizon and the depth of surface soil are highly correlated with site index of loblolly and shortleaf pines in the lower Piedmont of North Carolina.

A regression analysis between imbibitional water values of the subsoil and site index failed to show a significant relationship for the area in which this study was made. In order to eliminate a possible confounding effect of the littleleaf disease in reducing growth and thereby nullifying any relationship between site index and imbibitional water, another regression analysis was made between these two variables on only the 49 completely healthy shortleaf pine plots. No significant correlation was found between these variables. A lack of correlation may be due to the extensive soil degradation in this area or to the small number of healthy plots sampled.

A further analysis of the data by multiple regression shows that two variables—internal drainage and the difference in imbibitional water values between the surface horizon and subsoil—are highly correlated with site index. The relationship is significant at the 1 per cent level.[3] A coefficient of determination of 32.4 per cent was obtained. Small differences in imbibitional water values between the surface horizons and corresponding subsoils indicate a condition that may be termed "profile uniformity." Large differences indicate a lack of uniformity. For example, a soil with a coarse-textured sandy surface horizon and a heavy, relatively impervious clay subsoil would give a high value for this characteristic, and accordingly the site index would probably be low. A discussion of the importance of internal drainage is presented later.

TOPOGRAPHIC POSITION AND SITE INDEX

Five topographic positions were recognized in this survey: ridge top, upper slope, middle slope, lower slope, and bottoms. Average site indices for each topographic position were 59, 59, 61, 64, and 65 feet, respectively. The average percentage of littleleaf-diseased trees was 14, 13, 13, 14, and 14, respectively. No attempt was made to separate the influence of soil moisture or soil depth as they may be confounded with topographic position. Deeper soil and higher available moisture are probably largely responsible for the differences in site index. A greater recovery of *Phytophthora cinnamomi* from soil samples from the middle and lower slopes and bottoms was obtained than from the two higher topographic positions. This is probably due to higher amounts of moisture in these positions.

SILT-PLUS-CLAY CONTENT OF THE SURFACE SOIL AND SITE INDEX

The finer soil fractions included under this grouping represent all soil particles 0.05 mm. and less in diameter. Mechanical analyses of all soil samples were made by the Bouyoucos hydrometer method. For all plots, the mean percentage of silt-plus-clay for the surface horizon, averaging about 6 inches in depth, is 41 per cent, with individual values ranging from 21 to 81 per cent. There was no correlation between this factor and site index or littleleaf incidence. In many instances where erosion has been severe, the actual surface horizon is simply an accumulation of sand which had lost much of the finer material by erosion even before the land became established in pine forests.

SOIL EROSION, LITTLELEAF, AND SITE INDEX

Four erosion classes were recognized in this study: slight, moderate, severe, and rough gullied land. These classes are designated as 1, 2, 3, and 4 by the Division of Soil Survey Manual (1951). Littleleaf incidence and mean site index for the different erosion classes are shown in Table III.

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[3] The multiple regression equation derived for this relationship is: $Y = 89.79 - 6.63X_4 - 1.05X_{13} \pm 6.57$ where Y = site index, and X_4 is internal drainage values (rapid, moderate, slow, and very slow weighted numerically 2, 3, 4, and 5, respectively). X_{13} represents the difference in imbibitional water values between the surface horizon and subsoil.

TABLE III. *Littleleaf incidence and site index by erosion classes in shortleaf pine stands of the Piedmont*

Erosion class	Plots (no.)	Littleleaf trees (per cent)	Site index (feet)
Slight	12	4	62
Moderate	55	9	63
Severe	73	14	60
Rough gullied land	6	53	52

The various erosion classes were assigned numerical values, and a regression analysis made between the erosion classes and site index failed to show a significant relationship. It was quite obvious, however, that site index was very much lower on extremely eroded sites on which gullies had developed than on land with little erosion.

SOIL INTERNAL DRAINAGE, LITTLELEAF, AND SITE INDEX

Each of the 158 plots was classified as to internal drainage of the subsoil according to classes established by the Division of Soil Survey (1951), and placed into one of four classes: rapid, moderate, slow, and very slow, to which numerical values of 2, 3, 4, and 5, respectively, were assigned. A simple regression analysis showed a highly significant relationship between internal drainage and site index, and between internal drainage and littleleaf incidence. As subsoil drainage becomes slower, there is an accompanying increase in littleleaf and a decrease in site index of shortleaf pine stands. The internal drainage factor was also included in two multiple regression analyses along with 12 other independent variables using percentage of littleleaf trees in one case, and site index in the other as the dependent variable. In each analysis internal drainage was significantly correlated with each dependent variable.

Littleleaf incidence was highly correlated with internal drainage and soil erosion, the coefficient of determination being 0.37. In the case of littleleaf, the exposure of heavy-textured subsoils due to erosion and moist soil conditions provided by slow internal drainage favor a build-up of, and subsequent attacks by *Phytophthora cinnamomi* on the small roots of shortleaf pine.

Site index was also highly correlated with internal drainage and the difference between imbibitional water values of the surface soil and subsoil.

GROUND COVER COMPOSITION, LITTLELEAF, SITE INDEX, AND SOIL NITROGEN

Ground cover refers to the small plants 3 feet or less in height on each plot. It was classified into 17 classes based upon the predominant plants present. The abundance of ground cover was also recorded.

Table IV shows the classes of ground cover, with the corresponding site index, per cent of littleleaf trees, and total soil nitrogen content of the surface horizon. These data fell into 3 rather distinct groups. The first group was characterized by relatively low site indices, high incidence of littleleaf, and low soil nitrogen contents, and the chief component of the ground cover was broomsedge or grasses. Site indices in the second group fell at about the mean value for all survey plots. Littleleaf was generally much less, and surface soil nitrogen contents were higher than in the first group. Ground cover consisted chiefly of honeysuckle and herbaceous plants. The third group had site indices above the mean of all plots. The percentages of littleleaf trees were mostly low. Surface soil nitrogen contents were higher than in the preceding groups and the chief components of ground cover were honeysuckle, brambles, briers, and herbaceous plants. Wherever broomsedge or grasses were present in significant proportions, soil nitrogen was relatively low, and littleleaf tended to be high.

Since all abandoned land in the Piedmont quickly becomes covered by many of these plants, the lesser vegetation might serve as an indicator of the soil nitrogen level, and this may be taken as a general indication of site quality.

TABLE IV. *Ground cover composition, site index, per cent of littleleaf trees and soil nitrogen contents in South Carolina Piedmont shortleaf pine stands*

Main ground cover components	Plots (no.)	Mean site index (feet)	Littleleaf trees (per cent)	Total nitrogen, surface horizon (per cent)
Broomsedge	12	54	15	0.038
Broomsedge-grasses*	12	54	22	0.035
Broomsedge-brambles-vines-briers	28	56	18	0.049
Grasses	4	58	38	0.031
Herbaceous plants†	3	60	11	0.106
Broomsedge-herbaceous plants	39	60	15	0.055
Honeysuckle	5	61	2	0.070
Honeysuckle-grasses	4	61	9	0.036
Honeysuckle-brambles-vines-briers‡	6	62	6	0.063
Grasses-herbaceous plants	4	62	6	0.044
None (litter only)	5	64	2	0.062
Honeysuckle-smilax	1	65	0	0.083
Broomsedge-honeysuckle	13	66	10	0.059
Brambles-vines-briers-herbaceous plants	8	67	3	0.076
Brambles-vines-briers-grasses	5	67	18	0.037
Brambles-vines-briers	6	68	1	0.064
Honeysuckle-herbaceous plants	3	68	10	0.066

*Grasses or grass-like plants, excluding broomsedge.

†Herbaceous plants, *i.e.*, herbs, excluding grasses and shrubby plants.

‡Plants shrubby in nature.

CHEMICAL ANALYSES OF THE SURFACE HORIZON OF PLOTS

Soil samples of each separate horizon (usually A_p, A_2, B_1, B_2) were collected from 4 pits on each plot and were composited. From each large sample, a 1-quart composited horizon sample was air-dried and sieved for laboratory analysis.

Organic matter, replaceable hydrogen, potassium, calcium, magnesium, phosphorus, manganese, and active aluminum were determined according to methods outlined by Merkle (1940). Exchangeable cations were determined by a procedure devised by Brown (1943). The total exchange capacity was obtained by adding the exchangeable hydrogen as determined by Merkle's method to the cations determined according to Brown's procedure. With increasing site index there was a corresponding increase in soil organic matter and total soil introgen in the surface horizon. These two variables are themselves highly correlated, the correlation coefficient being 0.92 for the data for these plots. No relationship was found between the cation exchange capacity and site index. With one exception the cation exchange capacity of the various soils showed remarkable uniformity and ranged from 6 to 7 milliequivalents per 100 grams of dry soil. The per cent base saturation of the soils was variable but ranged near 40 per cent of the total cation exchange capacity, a figure clearly indicating low fertility.

SURFACE SOIL pH VALUES

Surface horizon pH values of 142 plots, or 90 per cent of all plots lie within the range of 1 pH unit, from 4.6 to 5.6. All values lie within the range of 1.8 pH units. No correlation was found between pH and site index or littleleaf incidence. The narrow range of pH values observed in the surface horizon points out the strong influence of climate and vegetation on soil processes in this area. Cultivated soils exhibit a greater range in pH than shown above, but after they have been abandoned and pine forests become established, the highly acidic organic matter produced by pines, coupled with intensive leaching of chemical bases under high rainfall, causes the soil to rapidly reach an equilibrium in pH value with that of the fallen surface litter.

SUMMARY

This report reviews soil and plant cover conditions as determined by a soils-littleleaf survey of 158 Piedmont forest stands consisting mainly of second-growth even-aged shortleaf pine.

Conclusions resulting from this survey are enumerated below:

1. The mean percentage of littleleaf trees in the 18 counties was 12.6. Abbeville, Fairfield, and Cherokee Counties in South Carolina, and Elbert County, Georgia, are very severe littleleaf areas.
2. The mean site index for the stands in the counties surveyed is 60.3 ± 0.49 feet.
3. Isolation of *Phytophthora cinnamomi* from soils varied widely, but an average of 25 per cent of the samples yielded the fungus. Isolation was most successful from moist, heavy-textured soils.
4. Certain deep well-drained soils consistently support shortleaf pine stands of high site index and relatively low littleleaf.
5. No relationship was found between aspect and littleleaf severity, but site index was higher on NW, SE, S, and SW slopes.
6. Of 13 soil factors analyzed by multiple regression, two factors—internal drainage and erosion—were highly correlated with the incidence of littleleaf. Among the same 13 soil factors, internal drainage and the difference in imbibitional water values between the surface soil and subsoil were highly correlated with site index.
7. No relation was found between littleleaf and topographic position. Site index was slightly higher on the lower topographic positions.
8. Neither littleleaf nor site index was correlated with the silt-plus-clay content of the surface horizon, or pH of the surface soil.
9. When the ground cover consisted chiefly of broomsedge or grasses, littleleaf severity was high, site index was generally low, and surface soil nitrogen was low. With a diminution in broomsedge and grasses in favor of herbaceous and shrubby plants, littleleaf was lower and site index and soil nitrogen were higher.
10. The fertility level of most forested Piedmont soils is low according to chemical tests for available nutrient elements.

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THE FACTOR OF TOPOGRAPHICAL CUES IN BIRD HOMING EXPERIMENTS

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Introduction

The problem of navigation by homing birds (especially pigeons) has during recent years received considerable attention. Several theories have been advanced to account for the "sense of direction" attributed to homing birds. Among the theories which attracted most attention were; the Coriolis force theory of Ising (1946) which was later extended and coupled with the theory of electro-magnetic effects by Yeagley (1947) and the infra-red vision theory of Wojtusiak (1949). In accordance with many other investigators, *e.g.* Thorpe (1949), Wilkinson (1949), Griffin (1952), we find that these theories are unacceptable, mainly because of the very great accuracy required in fixing the bird's position, evaluating its speed, determining and remembering very small changes in the forces involved, eliminating spurious effects, etc. The most recent of the theories of this type, namely the sun navigation theory of Matthews (1953a), is in our opinion also unacceptable, for the same reasons. G. Kramer (1953) performed some experiments to check this theory, but did not confirm Matthews' results.

Perhaps the most impressive work on the homing ability of birds has been done by D. R. Griffin (1944, 1949, 1952). Griffin distinguishes three levels of ability in birds' navigation. Type I navigation is the reliance on visual landmarks or in their absence the search for familiar territory by means of random flights or by a more or less systematic exploration. Type II navigation is the ability to fly in a particular direction, even in unfamiliar territory. In homing experiments with pigeons it is usually the direction of previous training that is followed for direction of flight in unfamiliar territory. Racing pigeons are trained in this way. Type III navigation is the hypothetical ability of a bird to head for the home locality even when released in unknown territory and when the correct direction of the homing flight bears no relation to directions that have previously been adhered to in training flights. This type of navigation appears to be the most baffling of all, as it seemingly requires a special "sense of direction" which would allow the bird to choose approximately the correct direction of its home even when it is released in a completely unknown territory.

The navigation of type II can be most plausibly explained by the assumption that the birds, when flying in the direction of a certain azimuth, may orient themselves by means of the sun (this sun orientation theory should not be confused with Matthews' sun navigation theory which implies the ability of the birds to determine their geographical location with respect to the loft and hence the course they have to take). Recently Kramer (1952) and his associates have reported direct experimental evidence for the theory of sun orientation. Kramer's ingenious laboratory experiments even suggest that birds are accustomed to making corrections for the sun's movement across the sky.

According to Griffin, the only convincing demonstration of the III type of homing was provided by Matthews (1951, 1953b), Kramer and St. Paul (1952) and Hitchcock (1952). A careful analysis of these experiments leads us to the conclusion that the results of these tests might be ascribed more plausibly to the ability of the birds to make use of topographical cues in an unknown territory (to a larger extent than it was assumed by other investigators). Thus in the present paper the arrangement and evaluation of the experiments of Matthews, Kramer and St. Paul, and Hitchcock are critically reviewed.

Experiments of Matthews

In 1948-52, G. V. T. Matthews of Cambridge performed a series of extensive experiments with homing pigeons and wild sea birds (Matthews 1951, 1952, 1953a, b).

The chief aim of these experiments was to check the homing ability when birds were released in an unknown territory. Matthews believes that the results of his experiments imply the existence of a special sense of orientation and he explains it by means of his sun navigation theory.

(Throughout the present paper the expressions "sense of direction" or "sense of orientation" are used instead of the hypothetical "ability of birds to determine their home course, when released in an unknown territory and without any previous training along this direction"; therefore, it does not imply necessarily the existence of a virtual sense located in some physiological organ.)

In brief the method Matthews used was as follows: In all the experimental flights the birds were released singly, each bird being released only when the preceding bird had vanished from sight. The birds were followed with binoculars until they vanished from view and then the bearing of this "vanishing point" was recorded. As an individual index the vanishing point may be somewhat misleading, but with a number of birds a departure "fan" is obtained, the orientation of which, in Matthew's opinion, may be interpreted with confidence.

The general arrangement of Matthews' experiments on pigeons in 1949-52 was the following. The lofts were situated near Cambridge. The birds were trained along the NNW direction, the distance between stages being successively increased. Afterwards the birds were released off the training line (*e.g.* test 8, 9) and in many cases Matthews found a significant (from the standpoint of statistical calculation) concentration of the vanishing points around the home direction.

We are unable to discuss in this paper all the experiments reported by Matthews. We would like only to show, by some examples, how the distribution of vanishing points was influenced by local topographical conditions. In our opinion, this factor was not given sufficient consideration and, therefore, we find ourselves unable to agree with the conclusions he drew from his experimental data.

In test 9, the release point was situated somewhere in Kent (Fig. 1) at a distance of 17-20 miles from the sea (seacoast and in S and SE directions, with land gradually shelving down towards the coast). Thus the birds, on a sunny day, were presumably able to see the sea from an altitude of no more than 200-300 feet beyond the release point. On the other hand the birds could not see the sea in north and north-east directions because of high hills. In our opinion these topographical conditions resulted in an almost regular fan of the vanishing points in all the directions where the sea could not be seen. Accidentally the home direction was almost at the centre of this fan, and so coincided with the average azimuth of the vanishing points.

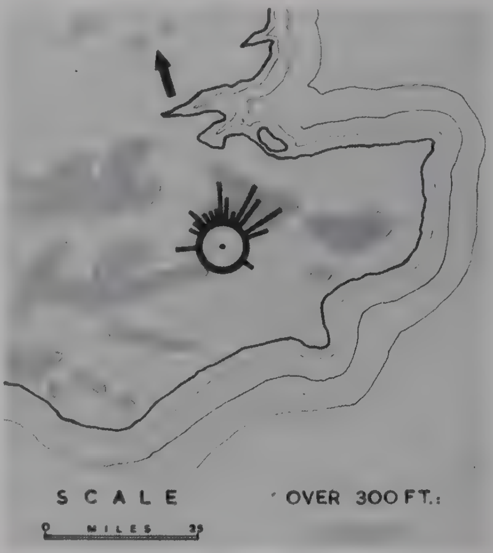

FIG. 1. Matthews' experiments. The distribution of vanishing points in test 9 superimposed on the contour map. The arrow indicates home direction.

In test 8 (Fig. 2) the release point was situated in the Upper Thames Valley which represents a more hilly landscape than the home country of the pigeons (near Cambridge): therefore, the birds apparently tried to get into more open land along two most promising directions; SE along the course of the Thames, and ENE over the flat land around Buckingham (compare the distribution of vanishing points in Fig. 2). As the home direction lay between these two preference courses it was again not far from the mean azimuth of the vanishing points.

When the birds were released from the same points but with an overcast sky (*e.g.* tests 20, 21 and others) the distribution of the vanishing points was almost random. Matthews did not report the conditions of visibility in these tests, but it may be supposed that the visibility was reduced, the sea not shining, etc., therefore the birds

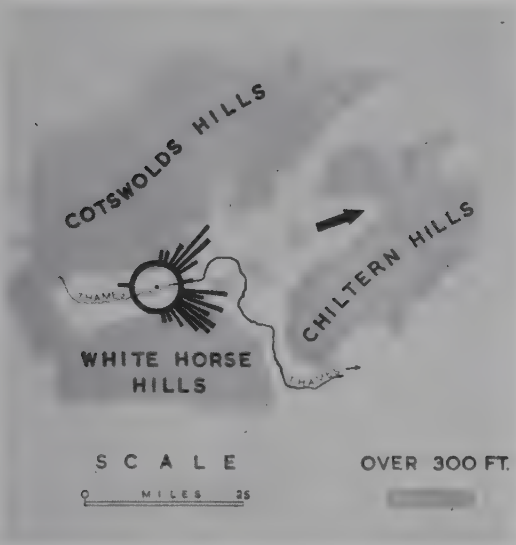

FIG. 2. Matthews' experiments. The distribution of vanishing points in test 8 superimposed on the contour map. The arrow indicates home direction.

could not make use of topographical cues and probably this fact resulted in random exploration.

It should be mentioned that in an experiment performed in 1950 from the same release point as in test 9 (Fig. 1) Matthews apparently obtained a quite reversed result, *i.e.* the birds seemed to head southwards. But this experiment, designed especially to prove Matthews' sun navigation theory, was conducted after a period of incarceration of the birds (with artificial light only), and Matthews did not perform any control experiments to check the possible effects of such an incarceration (for instance the vision of the birds could have been affected). As already mentioned Kramer's experiments performed under similar conditions (1953) did not confirm Matthews' results.

We would also point out that all the experiments based on the vanishing points method appear to be rather unreliable. The birds often circle at or beyond the limits of visibility, and so, when having momentarily lost the bird from sight, the observer may record a vanishing point, though in fact the bird has continued its circling flight and eventually disappeared in a quite different direction.

We found an influence of topographical cues also in others of Matthews' experiments with pigeons. In many cases, as for instance in the above-described tests 8 and 9, the statistical indices of the correlation between the vanishing point distribution and the topographical configuration of the terrain around the release points are much higher than those of the postulated link between the departure fans and loft direction.

Matthews has also conducted some experiments with the homing of wild birds, namely gulls (1952) and Manx shearwaters (1953b). When analysing these experiments we found a number of release points to lie within territory which probably was familiar to the birds, and this fact might have greatly influenced the total result. Moreover, the location of certain release points indicates that in many cases the home direction coincided with the "natural" direction of the flight, *i.e.* toward the sea, along the coastline, etc. We found also that in most cases the direction of the wind favoured the homing direction (the flight of all soaring birds is largely affected by wind). These factors were also not taken into account in the evaluation of the experiments.

(*Note:* the preceding paragraphs represent only a brief summary of an extensive study of all the experimental reports available, space considerations preventing a detailed discussion in this paper.)

EXPERIMENTS OF KRAMER AND ST. PAUL

Two German investigators, G. Kramer and U. von St. Paul (1952) performed experiments with pigeons released (in groups) far away from their loft in a completely unknown territory.

The loft was situated near Wilhelmshafen. Some of the birds had had training flights at a distance of less than 100 miles in the direction from the land toward the sea.

In the first experiment the birds were released at Giessen (200 miles south).

According to Kramer: "The starts of all the eight groups of the first flight were so strictly directional that there is little doubt that the birds were already orientated before starting—."

But he apparently overlooked the fact that Giessen is situated in the narrow valley of the Lahn River (Fig. 3) and though Lahn forces its way in a south-west direction between Westerwald and the Taunus mountains (up to 3000 ft.) this breach cannot be seen from Giessen and the most convenient "way out" of the valley is that chosen by the birds, namely the northerly direction over Marburg leading subsequently to Kassel. From Kassel onwards the birds had merely to follow the course of the river Weser and this was probably the reason why the homing in this test was so good (from 46 pigeons released at Giessen, 32 homed on the release day, and only 7 were lost).

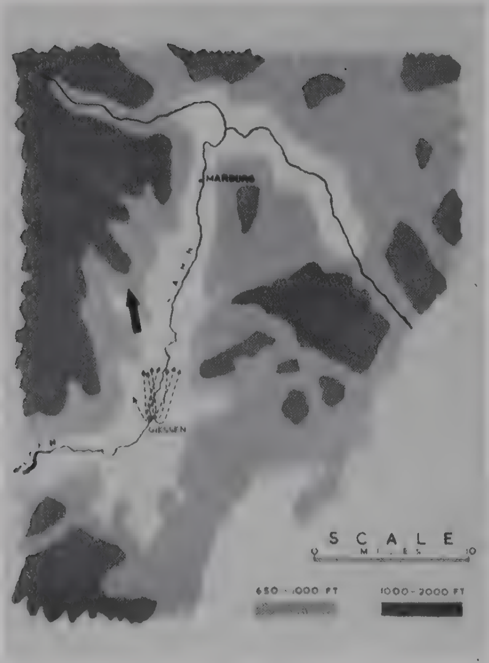

FIG. 3. Experiments of Kramer and St. Paul. The directions of the flight of pigeon groups superimposed on the contour map of the valley of the Lahn River. The arrow indicates home direction.

In the second release from the island of Fehmarn (130 miles) visibility conditions were excellent. The birds (released also in groups) at first circled near the release point and then headed toward the mainland (see Fig. 4).

"Getting so decidedly away from the island constitutes in itself evidence that the birds were orientated to a certain extent. A pigeon which had not the slightest idea where it was would first of all have examined the island—." But Kramer again overlooked the fact that under excellent conditions of visibility, the birds were quite able to see from an altitude of some 200 ft. that Fehmarn (diameter about 15 miles) was an island, so there was nothing unusual in the fact that they headed at once towards the mainland.

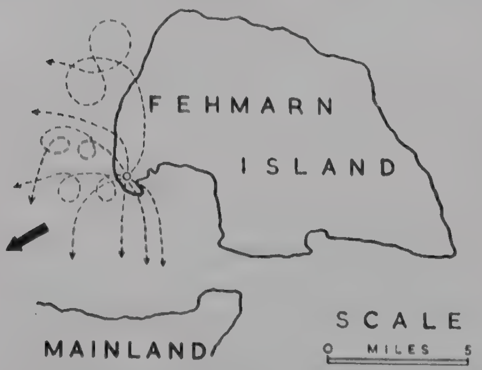

FIG. 4. Experiments of Kramer and St. Paul. The directions of the flight of pigeon groups superimposed on the map of Fehmarn Island. The arrow indicates home direction.

When the birds reached the mainland, probably an exploration (chiefly along the coastline) took place which resulted in a poor homing, because of very confusing geographical location of the release point (on the other side of the Jutland Peninsula). From 51 pigeons only 18 homed on the day of release, and 23 were lost.

Likewise a number of experiments of other investigators resulted in poor homing though the initial orientation of the birds seemed to be quite good. Since any reasonable concept of the "sense of direction" should require that it should work better at short distances, a flight commenced in approximately the correct direction should be successful. As this is often not the case, this fact seems to constitute an additional piece of evidence against any "sense of direction" theory, and indicates that the initial good "homing orientation" may be caused by other factors.

AEROPLANE OBSERVATIONS OF HOMING BIRDS

In the experiments discussed in the preceding sections of this paper only the direction of flight from the release point and the homing time have been noted. The obvious shortcoming of this method is that nothing is known of the route taken by the birds after their disappearance from the release point. To overcome this gap Griffin pioneered in using aeroplanes in following homing birds. In 1949 Griffin and Hock were successful in following gannets long distances. The most important experiments with aeroplane observations reported to date were those of H. B. Hitchcock (1952). He observed many flights of pigeons trained at Middlebury, Vermont, U.S.A. The village of Middlebury lies in the Lake Champlain valley between Adirondack Mountains (up to 4000-5000 feet) and Green Mountains (2000-4000 feet); the loft was located 12 miles east of Lake Champlain, near Otter Creek, a stream averaging 100 feet in width. Lake Champlain, narrow and elongated in a north-south direction (about 100 miles) represented a very characteristic landmark.

In Hitchcock's opinion his experiments have supported the theory of the existence of a special "sense of direction" (but he does not formulate any hypothesis about the physical nature of this sense). He maintains that the homing flight was definitely orientated toward the loft from the beginning (disregarding the orientation flight from the release point). He says that no consistent tendency to follow geographical landmarks was observed.

We suggest a different interpretation of these very valuable experiments. Let us examine, for instance, the diagram of the initial training flights (Fig. 5). In our opinion, a paramount influence on the homing routes was exerted by the course of Otter Creek, and by the chain of Green Mountains. When released in an unfamiliar mountainous valley the birds accustomed to a more open territory just seemed to strive to get away from the mountains. Thus the direction of the homing flight in its first stage might be described roughly as descending from the mountains. In some cases that course led almost directly to the loft. In other cases the birds eventually reached the familiar Otter Creek and only then turned toward the loft (see FIG. 5).

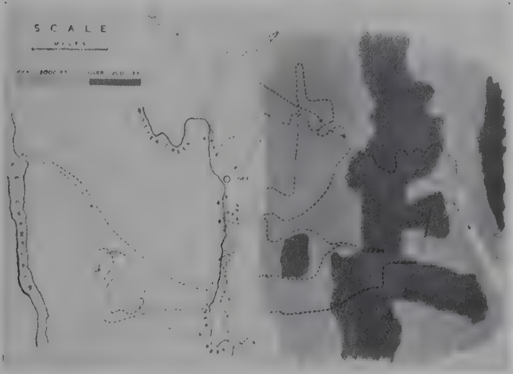

FIG. 5. Hitchcock's experiments. Training flights near Middlebury superimposed on the contour map of the valley of Lake Champlain.

The flights from a completely unknown territory, have not, in our opinion, corroborated the theory of the "sense of direction." In all these experiments the directions of flight were apparently not related to the home direction (at least the relation was not statistically significant); they were rather erratic or influenced by geographical cues or the conditioning by the previous directional training (this was also noticed by Hitchcock). The conditions of orientation (and the homing successes) were very good so long as the release points (in training flights) were situated in the Lake Champlain Valley or in the adjacent parts of Adirondacks and the Green Mountains. In the subsequent flights when the release points were situated outside that region, the orientation was very difficult. The percentage of successful returns in these experiments was very low, and hence, these returns might be ascribed to random exploration.

SUMMARY AND CONCLUSIONS

The results of the experiments of Matthews, Kramer and St. Paul, and Hitchcock, which had been regarded by some investigators as evidence for a special "sense of direction" in homing birds, have been critically analysed.

It has been suggested that in some of these experiments the seemingly positive results were due, at least partly, to the influence of topographical cues, which were not taken into account in the evaluation of the experimental data (Matthews, Kramer).

In the reports of other experiments (Hitchcock) no evidence could be found that the pigeons had, in fact, exhibited any special ability to home from unfamiliar territory. It is suggested that Hitchcock's report contains evidence that the pigeons were influenced to a considerable extent by topographical cues. Thus, when it is intended to investigate other factors assumed to influence the bird homing, the experiments should be planned in such a way as to eliminate any interference by topographical cues. If, however, such an elimination, is impossible, then this factor should be taken fully into account when evaluating the results of the experiments.

Very interesting experiments were performed by Griffin (1952) on the influence of topographical cues on the initial direction of the flight of pigeons when released in an unknown territory. He "fooled" the birds by releasing them near a lake very similar to the lake near which the birds were bred and trained. Whilst the results of these experiments were indicative, they were not conducted on a sufficiently large scale to be conclusive. We feel that more experiments of this type should be organised.

Footnote: Recently J. G. Pratt and R. H. Thouless have published the results of their experiments with homing pigeons (J. Exp. Biol., **32**: 70-83, 140-157, 1955). Their observations and remarks on the influence of the environment of the release point as related to the distribution of vanishing points (*e.g.* pp. 148-149) are completely in accord with the views expounded in the above article. They suggested that for the purpose of determining the significance of the experimental results each of the release points should be treated as a separate statistical unit. From this point of view their results were inconclusive because the number of release points was too small.

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DECIDUOUS FORESTS OF PONEMAH POINT, RED LAKE INDIAN RESERVATION, MINNESOTA

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The deciduous forests of Minnesota have been represented as a narrow belt running from the southeast to the northwest (Upham 1884, Rosendahl and Butters 1928, Daubenmire 1936, and Buell and Wilbur 1948). This belt lies between what is mapped as prairie on the west and coniferous forest on the east. As is generally true of vegetational transitions, the boundaries of these zones are seldom sharp. This is especially true of the transition to coniferous forest.

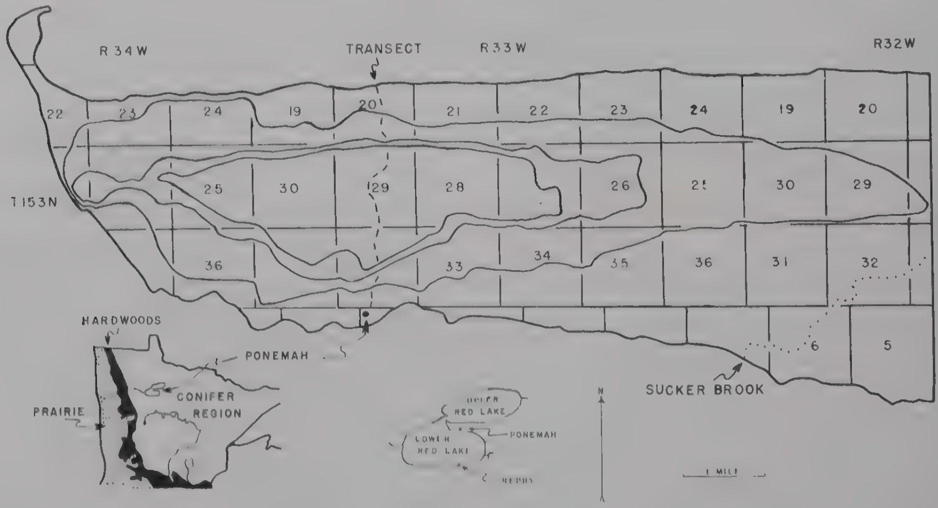

Fig. 1. Topographic map of Ponemah Point (approx. 48°N, 95°W) with generalized contours at about 50 foot intervals. The lake is 1170 feet above sea level. Several small isolated hills in the central part of the peninsula are slightly over 1400 feet elevation. The main road runs close to the south shore along the entire length of the Point. Certain section numbers have been included for orientation. Inset shows the location of this area on the vegetation map of northern Minnesota.

Within the deciduous belt, the coniferous forest occurs as small islands; eastward, it gradually becomes the continuous phase while the hardwoods are represented as insular stands which become more and more widely scattered toward the northeast (Butters and Abbe 1953). This picture is complicated by mixed conifer-hardwood stands (Grant 1934) and vast successional forests dominated by aspen which occupy areas where coniferous forests have been removed by cutting and burning.

The deciduous forests of Ponemah Point (Peninsula), located in northwestern Minnesota (48° N., 95° W.), represent an island of broadleaf trees in a matrix of coniferous forest (Fig. 1). They are of ecological interest because certain stands are among the most magnificent of the original deciduous forest still existing in the state, and since some stands seem to be expanding on cut-over lands formerly occupied by coniferous forest.

The peninsula is wholly within the bounds of the Red Lake Indian Reservation. Ponemah, a small village near the western tip of the peninsula, was settled by Chippewa Indians about 1864. Although clearings of approximately 100 acres have been made in the vicinity of the village and at a few spots along the southern shore, most of the Point has been left in woods. The occasional Indian huts in little openings accentuate the massiveness of the surrounding forest (Fig. 2).

The peninsula, a disjunct portion of calcareous terminal moraine of late Wisconsin (Mankato) time, is a tongue of land almost separating Upper and Lower Red Lake, relicts of glacial Lake Agassiz. During the early stages of Lake Agassiz, the raised central portion of the Point was an island. Near Redby, on the south shore of Lower Red Lake, three former beaches of the "Herman Series" are represented at 1,270, 1,246, and 1,220 feet above sea level (Leverett and Sardeson 1932). These old lake shores are also discernible on the Point.

The hardwood forests occupy the relatively level areas adjacent to the present shore line of the peninsula. The higher central part, which until the early 1900's supported splendid forests of white and red pine (*Pinus strobus* and *P. resinosa*), is now largely covered by white birch, aspen, and red maple (*Betula papyrifera, Populus tremuloides, P. grandidentata* and *Acer rubrum*). The low-lying east end is covered by aspen, spruce-fir (*Picea-Abies*), and bog forests. The Indians have harvested most of the red and white pine although scattered remnants still remain. Only one attempt has been made to cut the hardwoods for lumber, when, late in 1948, the timber north of the road on section 2 was cut.

The principal objective of the present study was to describe these unusual hardwood forests before further destruction should take place. It was also hoped that detailed study might result in some interpretation of their past history, and that successional trends might be discovered which would reveal the relationship of the hardwood communities to each other and to the contiguous conifer forests.

The authors are indebted to Dr. D. B. Lawrence for his critical reading of the manuscript.

METHODS

Detailed studies were made in a sugar maple-basswood stand (located west of Ponemah S. 35-36 R. 34 W.T. 153 N.) and a basswood-fir-black ash stand (located west of Sucker Brook in the south half of S. 35 R. 33 W.T. 153 N.). In both,

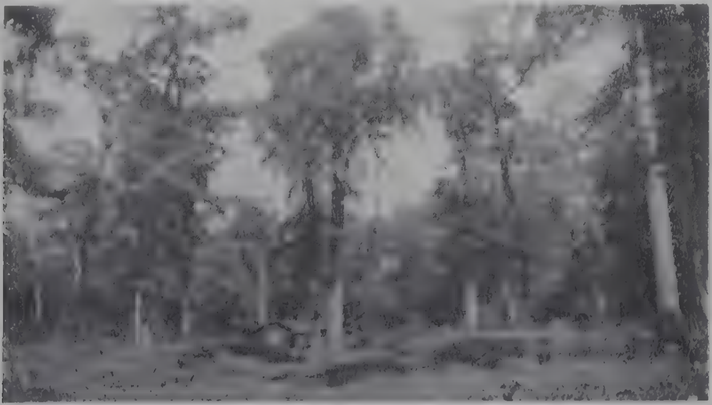

FIG. 2. A partial clearing along the main road a short distance west of Sucker Brook showing large elms.

10 m. x 10 m. quadrats were laid out at regular intervals along a base line. Ten quadrats were used in the sugar maple-basswood, and 25 in the basswood-fir-black ash stand. In each quadrat, the diameter was recorded by species of all trees 1″ or more d.b.h. Tree saplings (individuals 1′ high but less than 1″ d.b.h.) were counted on 2 m. x 10 m. plots established along the base line within the larger quadrats. A count of tree seedlings (individuals less than 1′ high) was made on ½ m. x 2 m. plots located 1 in each corner of the largest quadrats. Herb cover, moss cover, and unoccupied space were also tallied from the small quadrats. Herb cover was estimated by species, but the cover of mosses was recorded independent of species and listed as "moss cover." Shrub cover was measured by the line intercept method along a 20 m. line established diagonally across each quadrat and beyond. In addition, tree cover in the basswood-fir-black ash stand was measured by the line intercept method (Buell and Cantlon 1950) along two 125 m. lines, and along two 100 m. lines in the maple-basswood stand. In both stands, several soil pits were dug and descriptions of the profiles were recorded. Samples of each horizon were obtained and later analyzed for texture by the hydrometer method (Bouyoucos 1936). Soil pH was determined colorimetrically (hydrion papers) in the maple-basswood stand and electrically (Beckman glass electrode method) in the basswood-fir-black ash stand.

A transect was made across the peninsula along the road that runs directly north from Ponemah. At $\frac{1}{10}$ mile intervals, measured by an automobile mileage recorder, 5 m. x 20 m. plots were established 20 m. away from the road. At a few stations that were excessively disturbed only general notes were made. On the plots, diameters of all trees 1″ d.b.h. or over were recorded by species. Tree saplings were recorded by species on 2½ m. x 2 m. plots in each corner of the 5 m. x 20 m. quadrats. To these measurements were added general observations on the vegetation surrounding each quadrat, along with notes on disturbance from such causes as lumbering, fire, and grazing. In addition soil pits were dug, a profile description was made, and a sample of each horizon was taken for mechanical analysis.

Nomenclature for trees and shrubs is according to Rosendahl and Butters (1928) and for herbs according to Fernald (1950) except where the authority is given.

Most of the field work was done during August of the summers of 1948 and 1949. Two visits were made to the area in 1952.

RESULTS

Vegetation

Sugar maple-basswood stand.—In the sugar maple-basswood stand basswood (*Tilia americana*) outranked all other tree species in basal area but not in the number of individuals (Table I). The density of sugar maple (*Acer saccharum*) was greater in the largest size class, although basswood was represented by larger trees than sugar maple. The largest basswood measured 30″ d.b.h., while the largest sugar maple was only 17.5″ d.b.h. There were some seedlings of the latter, but basswood seedlings were not found in any of the quadrats. Basswood, however, char-

TABLE I. *Density, frequency, basal area and per cent of total basal area for all size classes of trees in the sugar maple-basswood forest. Data based on 1,000 square meters (seedling density has been multiplied by 25 and sapling density by 5)*

Species	Seedlings <1′ high		Saplings > 1′ high <1″ d.b.h.		Trees from 1″ to 3.9″ d.b.h.				Trees 4″ or more d.b.h.				All trees >1″ d.b.h.	
	Density	Frequency	Density	Frequency	Density	Frequency	Basal Area in sq. ft.	% B. A. in Size Class	Density	Frequency	Basal Area in sq. ft.	% B. A. in Size Class	Basal Area in sq. ft.	% Total B. A.
1. *Tilia americana*	—	—	75	30	26	70	0.47	41.2	14	50	15.97	48.8	16.44	48.5
2. *Acer saccharum*	100	25	100	90	10	50	0.33	28.9	15	90	7.29	22.3	7.62	22.5
3. *Ulmus americana*	—	—	5	10	1	10	0.03	2.6	3	30	5.20	15.9	5.23	15.4
4. *Ulmus fulva*	—	—	30	30	2	20	0.11	9.6	5	50	3.97	12.1	4.08	12.0
5. *Acer negundo*	—	—	45	10	1	10	0.06	5.3	2	10	0.32	1	0.38	1.1
6. *Fraxinus nigra*	—	—	25	20	2	10	0.08	7.0	—	—	—	—	0.08	0.2
7. *Celtis occidentalis*	—	—	15	20	1	10	0.06	5.3	—	—	—	—	0.06	0.2
8. *Ulmus* spp.	50	25	—	—	—	—	—	—	—	—	—	—	—	—
Totals	..	..	..	..	..	..	1.14	..	..	..	32.75	..	33.89	..

acteristically perpetuates itself effectively by stump sprouts. The only other trees of importance were the elms (*Ulmus americana* and *U. rubra*). Both were represented in all size classes but the seedling class. Box elder (*Acer negundo*), black ash (*Fraxinus nigra*), and hackberry (*Celtis occidentalis*) were of minor importance.

The mean height of the forest determined by measuring several trees was about 17 meters. The top of the canopy was relatively uniform since the dominants were approximately the same height and was practically continuous with only 4% of its area represented by gaps (unoccupied space in Fig. 3).

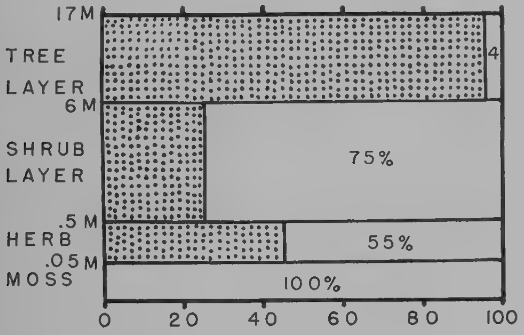

Fig. 3. Cover diagram for the sugar maple-basswood stand. Vertical bar gives approximate heights in meters. Horizontal bar gives per cent cover. Figures to the right of the bars represent the per cent unoccupied space or area in each layer.

Table II. *Cover and frequency of shrubs and herbs in the sugar maple-basswood stand. Due to overlapping by species, percentages of actual cover may total over 100%. Frequency refers to per cent occurrence on line transects for shrubs, on quadrats for herbs. Only the principal species are included*

	Per cent of total vegetation cover	Per cent of actual ground cover	Frequency
Shrubs:			
A. Space (no cover)	—	75	—
1. *Acer spicatum*	55	19	80
2. *Prunus virginiana*	31	11	80
3. *Corylus rostrata*	9	3	30
4. *Cornus alternifolia*	2	1	20
Herbs:			
A. All Herbs	—	55	—
B. Space (no cover)	—	45	—
1. *Laportea canadensis*	69	38	88
2. *Osmorhiza claytoni*	12	7	48
3. *Uvularia grandiflora*	6	4	65
4. *Smilacina racemosa*	3	2	38
5. *Rudbeckia laciniata*	2	1	75
6. *Arisaema triphyllum*	3	2	50
7. *Carex pensylvanica*	2	1	28

The shrub layer of this community was relatively sparse—only 25% of its area was covered (Fig. 3). *Acer spicatum* and *Prunus virginiana* were by far the most important species; *Corylus rostrata* and *Cornus alternifolia* were of less importance (Table II). Four other species, *Sambucus pubens, Ribes cynosbati, Celastrus scandens,* and *Pathenocissus vitacea* were present but contributed only 1% or less of the cover.

The herb layer had 55% of its area unoccupied (Fig. 3). Of the herbs present, *Laportea canadensis* with 38% cover was primarily responsible for the ground aspect. Toward the lake away from the maple-basswood stand, the forest composition changed to elm-basswod dominance and *Laportea* increased considerably forming a dense herb layer about a meter high. Six other species, *Osmorhiza claytoni, Uvularia grandiflora, Smilacina racemosa, Rudbeckia laciniata, Arisaema triphyllum,* and *Carex pensylvanica,* contributed appreciably to this layer (Table II). Of less importance were 13 species of herbs which occurred in the quadrats but together made up only 2% of the cover. In order of decreasing importance, these were *Caulophyllum thalictroides, Polygonatum biflorum, Oakesia sessilifolia, Hystrix patula, Allium tricoccum, Festuca nutans, Carex pedunculata, Sanguinaria canadensis, Equisetum* spp., *Streptopus longipes, Circaea intermedia, Trillium grandiflorum, Viola pubescens,* and *Osmorhiza longistylis. Allium tricoccum,* with a frequency of 40%, had only fruit stalks showing in August when the field work was done. In the spring, when its leaves are present, its contribution to cover would be higher.

This sugar maple-basswood forest was open and easy to travel through in spite of frequent fallen, decaying trees. It and the elm-basswod with which it merged occurred with some variation through the southern portion of the peninsula from the vicinity of the village westward to the point and along the north shore from about section 20 to section 24 range 33. Sugar maple-basswood appeared at both ends of the transect (Figs. 1 and 7). Probably an essentially similar type of forest once occupied the area where the village now stands, as well as the higher land along the lake east of the village. There and in other places the land was cleared following settlement and used for agriculture, but some of the larger elms were left standing (Fig. 4). With the de-

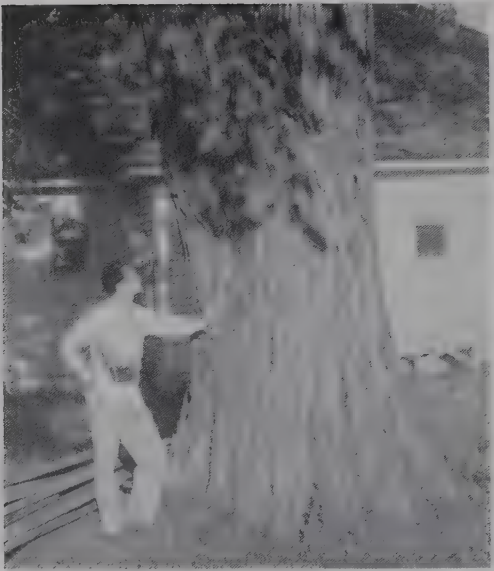

FIG. 4. An American elm, 57 inches d.b.h., on the Ponemah school grounds.

velopment of commercial fishing and increased use of canned foods, the Indians have practically abandoned agricultural pursuits, and secondary successions have been initiated.

In some places where the maple-basswod community was richer in maples, especially along the north shore of the peninsula, the Indians collected maple sap. Their method of tapping trees by making a slanting cut near the ground with a hatchet caused considerable deformation of the tree bases.

Basswood-fir-black ash.—Certain stands were designated basswood, balsam fir (*Abies balsamea*), and black ash stands since these species were by far the most important species in them. One such stand was studied in detail. Not only were the basswood, balsam fir and black ash high in their contribution to basal area but were present in all size classes (Table III). American elm (*Ulmus americana*) and white birch (*Betula papyrifera*) were important as mature trees together composing over 36% of the total basal area of trees over 10″ d.b.h. In addition, there were many large dead birch trees. However, neither the elm nor the birch seemed to be reproducing effectively. Although elms were present as seedlings none was found between the seedling size and trees 4 inches d.b.h. or over. Only one small paper birch was found. Six others trees contributing to the canopy failed to show ability to reproduce successfully in this stand (Table III). Sugar maple was present only as scattered young trees. The canopy was almost continuous, only 10% of its area was represented by gaps between the tree crowns (Fig. 5).

The mature trees averaged well over 200 years in age. In the portion of the stand cut between the summers of 1948 and 1949 ring counts were made on the stumps with the following results (diameters at stump height, about 1 m.): white birch 35″, 110 years; black ash 24.5″, 252 years;

TABLE III. *Density, frequency and basal area and per cent of total basal area of all size classes of trees in the basswood-fir-black ash forest. Density and basal area figured on the basis of 1,000 square meters (2,500 square meter sample. Seedling density has been multiplied by 10)*

Species	Seedlings <1′ high		Saplings >1′ high, <1″ d.b.h.		Trees of 1″-3.9″ d.b.h.				Trees of 4″-9.9″ d.b.h.				Trees of >10″ d.b.h.				All trees >1″ d.b.h.	
	Density	Frequency	Density	Frequency	Density	Frequency	Basal Area in sq. ft.	% of Total B. A. in 1″-3.9″ Size Class	Density	Frequency	Basal Area in sq. ft.	% of Total B. A. in 4″-10″ Size Class	Density	Frequency	Basal Area in sq. ft.	% of Total B. A. in >10″ Size Class	Total B. A. of all Trees >1″ d.b.h.	% of Total Basal Area
1. *Tilia americana*	20	8	40	16	8.8	36	0.30	14.5	4.8	28	1.20	17.3	5.2	32	6.24	21.9	7.74	20.6
2. *Abies balsamea*	90	20	96	60	52.0	84	1.54	74.4	12.8	64	2.34	33.7	1.6	24	1.18	4.1	5.07	13.5
3. *Fraxinus nigra*	570	40	148	44	8.4	36	0.22	10.6	6.4	28	1.44	20.7	2.4	24	3.11	10.9	4.77	12.7
4. *Ulmus americana*	12920	88	—	—	—	—	—	—	3.2	20	0.99	14.2	6.4	52	6.28	22.0	7.27	19.4
5. *Betula papyrifera*	20	8	—	—	0.3	4	0.01	0.5	1.2	8	0.43	6.2	3.2	24	3.99	14.0	4.44	11.8
6. *Quercus macrocarpa*	20	4	—	—	—	—	—	—	—	—	—	—	1.0	12	2.57	9.0	2.57	6.8
7. *Picea canadensis*	—	—	—	—	0.4	4	—	—	0.8	8	0.31	4.5	0.8	8	1.73	6.1	2.04	5.4
8. *Populus balsamifera*	—	—	16	12	—	—	—	—	—	—	—	—	0.8	8	1.60	5.6	1.60	4.3
9. *Pinus strobus*	—	—	—	—	—	—	—	—	—	—	—	—	0.4	4	1.51	5.3	1.51	4.0
10. *Fraxinus pensylvanica*	—	—	—	—	—	—	—	—	0.4	4	0.07	1.0	0.4	4	0.30	1.1	0.38	1.0
11. *Ulmus fulva*	—	—	—	—	—	—	—	—	0.4	4	0.17	2.4	—	—	—	—	0.17	0.5
12. *Acer saccharum*	10	4	—	—	0.4	4	—	—	—	—	—	—	—	—	—	—	—	—
Totals	..	..	..	..	..	..	2.07	..	..	..	6.95	..	..	..	28.51	..	37.56	..

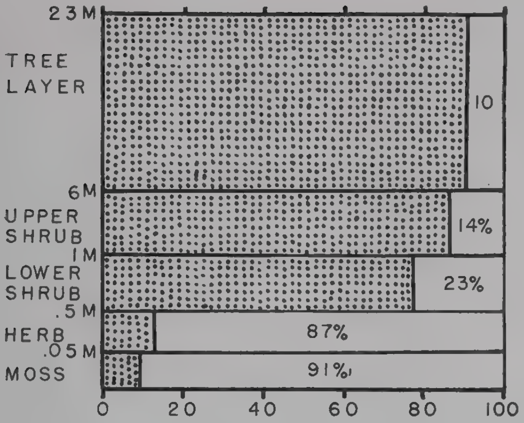

FIG. 5. Cover diagram for the basswood-balsam fir-black ash stand. Vertical coordinate represents approximate heights in meters. Horizontal coordinate gives per cent cover. Figures to the right of the bars represent the per cent unoccupied space or area in each layer. Two shrub layers are shown because of the pronounced development of two strongly contrasting dominants, *Acer spicatum* and *Taxus canadensis.*

23.0″, 200 years; 23.7″, 288 years; 22″, 231 years; 23.5″, 181 years; 23.4″, 250 years; bur oak (*Quercus macrocarpa*) 21″, 200 years; American elm 22.5″, 215 years; 22.5″, 200 years; 26.2″, 227 years. It seemed likely that the uncut portion was probably the same age.

The height of the forest averaged about 23 meters. Five trees of balsam fir measured 12.5″ d.b.h. and 23 m. high; 8.9″ d.b.h. and 13 m. high; 5.2″ d.b.h. and 8 m. high; 4.2″ d.b.h. and 8.7 m. high; and 5.7″ d.b.h. and 12.5 m. high. Three trees of black ash measured 16.9″ d.b.h. and 30 m. high; 4.7″ d.b.h. and 11 m. high; and 2.3″ d.b.h. and 7 m. high. Two trees of white spruce (*Picea glauca*) were 19.3″ d.b.h. and 22.5 m. high; and 22.5″ d.b.h. and 27 m. high. Two trees of basswood measured 18.5″ d.b.h. and 19.5 m. high; and 22″ d.b.h. and 23 m. high. A bur oak 21.5″ d.b.h. measured 11 m. to the first limb and 24 m. to the top of the tree. A white pine (*Pinus strobus*) 36″ d.b.h. measured 16 m. to the first branches and over 36 m. to the top of the tree. Due to the varying heights of the component species, the top of the canopy was very irregular.

The shrub layer primarily composed of *Acer spicatum* and *Taxus canadensis* was very dense; only 6.3% was unoccupied space (Table IV). Actually, these two species formed separate shrub strata, an upper layer of *Acer* extending to a height of 6 m. and a lower layer of *Taxus* extending to a height of about 1 m. Even when measured separately the cover values for these species were high (Fig. 5). Four other shrub species, *Rubus strigosus, Corylus rostrata, Celastrus scandens,* and *Prunus virginiana,* together made up 11% of the total shrub cover. Nine species, listed according to decreasing frequency, *Lonicera canadensis, Cornus alternifolia, Ribes cynosbati, R. triste, R. prostratum, Viburnun trilobum, Amelanchier humilis, Sambucus pubens,* and *Ribes hirtellum,* made but a minor contribution to shrub cover totaling only 2%. In addition, tree saplings contributed cover in this layer: *Abies balsamea,* 3%, *Fraxinus nigra,* 2%, and *Tilia americana, Populus balsamifera,* and *Betula papyrifera* each less than 1%.

TABLE IV. *Foliage cover and frequency of shrubs, herbs and mosses in the basswood-fir-black ash forest. Due to overlapping by species percentages of actual cover may total over 100%. Frequency refers to % occurrence on line transects for shrubs, in quadrats for the plants in the herb and moss layers. Only the principal species are included*

	Per cent of total cover	Per cent of actual ground cover	Frequency
Shrubs and tree Saplings:			
A. Space (no cover).....	—	6.3	—
1. *Acer spicatum*........	42.4	69	96
2. *Taxus canadensis*.....	39.2	64	100
3. *Rubus strigosus*.......	5.1	8	16
4. *Abies balsamea*.......	3.4	6	52
5. *Corylus rostrata*......	3.1	5	52
6. *Fraxinus nigra*.......	1.9	3	40
7. *Celastrus scandens*....	1.8	3	16
8. *Prunus virginiana*....	1.1	2	28
Herb and Moss Layers:			
A. Space (no cover).....	—	44.0	100
B. Moss..............	—	9.3	71
C. Herbs.............	—	12.7	75
D. Other (Low shrubs in the herb layer)....	—	44.0	—
1. *Uvularia grandiflora*..	18	2.2	24
2. *Carex pensylvanica*....	13	1.6	16
3. *Circaea alpina*.......	9	1.1	18
4. *Pteretis pensylvanica* (Willd.) Fernald...	8	1.1	13
5. *Carex pedunculata*....	7	1.0	28
6. *Aralia nudicaulis*.....	7	.9	14
7. *Schizachne purpurascens* (Torr.) Swallen	5	.7	5
8. *Arisaema triphyllum*..	4	.5	28

Herbs were relatively sparse, the estimate of their total cover being only 13% (Fig. 5). Unoccupied space in this layer was greatly reduced by the low branching shrub, *Taxus canadensis*, whose large spreading clones formed a very heavy cover (Table IV). The greatest cover attained by any herb was 2.2%, the figure obtained for *Uvularia grandiflora*. Only 7 other species, *Carex pensylvanica, Circaea alpina, Pteretis pensylvanica, Carex pedunculata, Aralia nudicaulis, Schizachne purpurascens,* and *Arisaema triphyllum*, reached or even approached an average estimated cover of 1% each (Table IV). Twenty-six other species collectively contributed only 3.6% cover in the herb layer. These are, listed in the order of decreasing frequency: *Viola blanda*, 32% frequency; *Galium triflorum*, 26%; *Dryopteris spinulosa*, 14%; *Streptopus longipes*, 13%; *Laportea canadensis*, 13%; *Maianthemum canadense*, 12%; *Asarum canadense*, 11%; *Mitella nuda*, 10%; *Rubus pubescens*, 5%; *Athyrium angustum* (Willd.) Presl., 4%; *Trientalis borealis*, 4%; *Impatiens biflora*, 3%; *Thalictrum dioicum*, 3%; *Dryopteris linneana*, 3%; *Osmorhiza claytoni*, 2%; *Cinna latifolia*, 2%; *Caulophyllum thalictroides*, 1%; *Viola conspersa*, 1%; *Botrichium virginianum*, 1%; *Clintonia borealis*, 1%; *Equisetum sylvaticum*, 1%; *Rhus radicans*, 1%; *Carex gracillima*, 1%; *Polygonatum biflorum*, 1%; *Oryzopsis asperifolia*, 1%; and *Trillium grandiflorum*, 1%. In addition, *Smilacina racemosa, Sicyos angulata, Aralia racemosa,* and *Smilax herbacea* were noted outside of the quadrats. Corms of *Dicentra* were seen frequently, although in the later part of the summer when the study was made no aerial parts of the plant were evident. In the summer of 1949, a magnificent display of tall vigorous plants of *Impatiens* was in bloom throughout the cut-over portion. In this population, *I. biflora, I. pallida,* and many seemingly intermediate types occurred side by side.

Cover in the moss layer was estimated at only 9% (Fig. 5).

The aspect of this basswood-fir-black ash forest was impressive. The great size of the deciduous trees was accentuated by small Indian clearings and the narrow canyon-like roads which cut through the forest. Its exceptional development was in marked contrast to the second-growth pine, aspen, young hardwoods, and muskegs of the surrounding area. Within the forest, the denseness and luxuriance of the undergrowth and smaller trees made travel, except along Indian paths, difficult.

The deciduous canopy was pierced by occasional spires of white spruce and balsam fir, while the large trunks of infrequent white pines disappeared through the uppermost foliage, their crowns spreading above those of the hardwoods.

This community occupied a strip of land north of the main road beginning at the east end of the peninsula and extending through sections 36, 35, 34, 33, and into section 32. Through this area, community composition changed with minor changes of topography. Toward section 32, sugar maple increased and the community merged into sugar maple-basswood, while toward the lake there was a shift to forest dominated by elm and basswood. Near Sucker Brook silver maple (*Acer saccharinum*) was occasionally found. One measured 37.5 inches d.b.h. (Fig. 6).

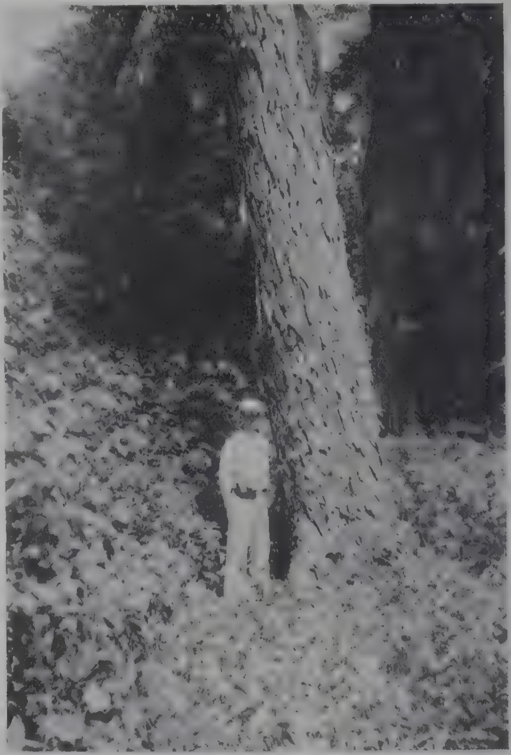

Fig. 6. A silver maple, 37 inches d.b.h., growing along the main road a short distance west of Sucker Brook.

The transect.—The transect across the Point from south to north started at the outskirts of Ponemah and crossed the peninsula near its highest elevation (Figs. 1 and 7). From Ponemah following the road north along this line, a fine sugar maple-basswood stand with scattered large bur oaks was immediately encountered. This old stand extended for about one-half mile; the sugar maple and basswood trees were younger.

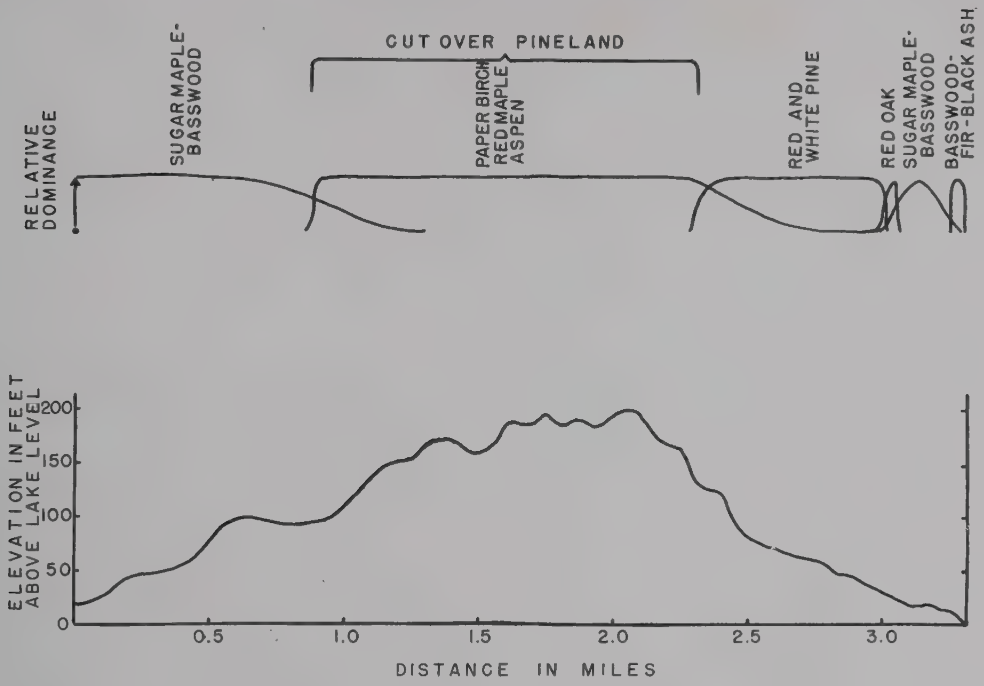

FIG. 7. A cross section of the peninsula along the route of the transect indicated in Figure 1. The upper portion of the diagram shows the occurrence of various plant communities along the transect.

After 0.9 miles, the sugar maple-basswood lost dominance to a paper birch-aspen (*Populus grandidentata* and *P. tremuloides*)—red maple (*Acer rubrum*) community. However, reproduction of sugar maple and basswood and of their associates continued to be present for nearly one and three-quarter miles from the beginning of the transect. The loss of sugar maple-basswood dominance roughly coincided with the margin of the cut-over pine land now covered by paper birch-aspen-red maple. This latter, second growth community, extended over the higher portions of the peninsula for a distance of approximately 1.4 miles. It was less important on the north side where a young forest of red and white pine (*Pinus resinosa* and *P. strobus*) occupied most of the middle portion of the north slope. In places, although not on the line of the transect, the pine forest gave way to a community in which red oak (*Quercus borealis*) was important. Further along the transect, the pine was replaced by moderately well-developed sugar maple-basswood. Beyond that to the north was a basswood-balsam fir-black ash community which covered the lowest area along the southern shore of Upper Red Lake.

These communities, crossed by the south-north transect, extended to a greater or lesser distance east and west along the peninsula. As already stated, the sugar maple-basswood at the north end graded eastward into basswood-balsam fir-black ash. The paper birch-aspen-red maple covered most of the backbone of the peninsula, but it was interrupted eastward in section 30 by bog land supporting spruce (*Picea*), cedar (*Thuja*) or low-lying spruce-fir forest which together occupied much of the east end of the peninsula. The pine forest on the north slope continued west well out toward the end of the point and eastward toward the lowland forests. Its extent coincided with an area which was severely burned over in the early part of this century. The same east-west pattern though less extensive held for the other communities, red oak, maple-basswood, basswood-fir-black ash, along the south shore of Upper Red Lake. However, they were less distinctive and less continuous as vegetation units. Often they graded into each other, and often they were highly mixed with aspen. Frequently they exhibited aspen dominance.

Soils

Sugar maple-basswood.—The soil beneath the sugar maple-basswood stand is illustrated by the following profile taken from a single trench.

F 1 cm. of fermented litter.
H 6 cm. of fine, black, crumbly humus grading imperceptibly into the mineral A horizon (pH 4.0).
A_1 7 cm. of blackish gray silt.
A_2 21 cm. of light-brownish gray silty, fine structureless sand which grades gradually into the B horizon (pH 4.5).
B 18 cm. of light brown silty clay which breaks down into irregular aggregates sometimes covered with a light gray surface deposit. Sharp transition to C horizon.
C A gravel containing some sand and clay with many stones ranging in size up to 5-8 cm. The stones are of many kinds including limestones. In the upper part of this horizon occasional lenses of reddish silty material with a black, greasy coating occur (pH 5.5-6.0).

This profile fits the description of a leached grood or a strongly degraded chernozem (Wilde 1946, Joffe 1949). Dr. Wilde has kindly examined the soil samples and has confirmed this determination in correspondence. In contrast with the soil under the basswood-fir-black ash stand, this soil has excellent subsurface drainage.

Basswood-fir-black ash.—The morphology of the soil underlying the basswood-fir-black ash may be illustrated by the following profile compiled from observations of four soil pits:

F 7-12 cm. poorly decomposed litter.
H 2-9 cm.
A 9-12 cm. of ashy gray loam or loamy sand sharply separated from the humus horizon (pH 6.3-6.9).
B 12-30 cm. of brownish loam or loamy sand with little or no textural difference from the A. In some cases this horizon is mottled in the lower portions (pH 6.3-7.3).
C Grayish loam to silty clay mottled toward the top and containing carbonates. This layer is extremely hard when dry (pH 6.5-7.8).

This soil fits the description of a gley soil (Wilde 1946) in which a gley horizon occurs within reach of the main root systems of the trees, in this instance being at a depth of 50 to 90 cm. The cause of this gley is probably a deep impervious stratum of boulder clay whose upper extent was encountered in one of the pits and whose depth was demonstrated in a nearby excavation.

The transect.—The soils along the entire length of the peninsula transect were found to be embryonic soils, gravelly sands with little horizon development. All showed a distinct tendency toward podzolization with mor humus layers. However, only a faint suggestion of the leached A_2 was to be found and this only under the sugar maple-basswood on the gentle south slope. In no case did textural analyses indicate a distinct textural difference between the leached A_2 and the zone of accumulation. At some sites a weakly developed sandy-clay layer 2-4 cm. in thickness was taken to indicate the beginning of the development of a true B horizon. At the north end of the transect an immature gley soil was found under a stand of basswood-fir-black ash.

DISCUSSION

Approaching Red Lake from the south one passes through a forest vegetation composed of a matrix of second growth aspen, birch, red pine, and jack pine, with localized stands of spruce-fir, scattered forests of bur oak and an occasional stand of sugar maple-basswood. With the exception of sporadic red pine stands, most of the trees are low in stature with relatively small diameters. The contrast between this vegetation and that of the Point is striking. The forest along the lower bench of the peninsula is almost wholly deciduous. In many places, the canopy extends to heights of 23 meters. In clearings made by the Indians, relict trees with diameters of two to three feet may be seen (Fig. 2). One elm in the village of Ponemah measured 57 inches d.b.h. (Fig. 4). Among these forests, the basswood-fir-black ash community is the most magnificent. Its old trees and its towering canopy place it among the most impressive deciduous forests in Minnesota. Although the maple-basswood forests are less spectacular, they are well-developed and compare favorably with similar communities growing in the western part of the "Big Woods" (Daubenmire 1936), in Itasca Park, and in Mahnomen County (Buell and Cantlon 1951).

In the western part of the "Big Woods," the maple-basswood forest occurs frequently on the eastern sides of lakes. Daubenmire (1936) ascribes their location to fire protection, the lake acting as a fire break. Although this may be the reason for the persistence of the deciduous forests on Ponemah Point we are inclined to believe that their presence and distribution is controlled by the variations in local climate and the calcareous nature of the terminal moraine forming the peninsula.

Rosendahl and Butters (1928) suggested that the lakeside occurrence of deciduous forest in the coniferous zone is to be explained by an extended growing season resulting from the ameliorating effect of the water and especially from the pre-

TABLE V. *Climatological data for Redby, Minnesota (previous to 1925, records were taken at Red Lake, 5 mi. west). Comparative figures for certain data are given for Itasca Park. Annual rainfall for Itasca Park is 23.63 inches with comparable monthly distribution. The annual snowfall for Itasca Park is 38.3 inches. Rainfall and snowfall are given in inches and temperature in °F. Data abstracted from Purssell (1934)*

	*	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Average precipitation	R	.67	.60	.82	1.36	—2.42	4.29	3.09	2.81	2.74	1.57	.95	.69	22.01
Snowfall	R	7.9	5.9	6.3	2.2	0.1	0	0	0	T	1.3	6.1	7.8	37.6
Average temperature	R I	1.8 2.0	7.9 8.3	22.5 22.2	40.1 40.1	52.7 51.8	63.0 61.0	68.1 66.0	65.3 63.0	57.3 54.7	43.9 42.3	27.2 27.8	11.9 11.5	38.5 37.6
Average max. temp.	R I	13.9 15.4	19.2 21.6	34.0 35.4	51.3 53.1	63.8 66.7	73.8 74.7	79.5 79.6	76.9 76.8	68.4 67.5	54.0 56.3	34.3 37.9	20.5 20.9	49.1 50.5
Average min. temp.	R I	− 8.6 −10.5	− 3.2 − 4.2	10.9 8.8	27.6 27.2	40.8 37.2	52.1 47.8	57.6 52.3	53.8 49.1	46.2 42.1	33.7 30.2	19.3 17.6	1.9 .4	27.7 24.8
Highest temperature	R I	48 48	58 59	80 75	88 88	94 96	99 100	109 105	96 101	96 95	86 89	67 66	48 54	109 105
Lowest temperature	R I	−46 −51	−48 −48	−33 −41	− 5 −11	17 16	30 25	35 32	32 26	18 17	0 −14	−27 −29	−44 −47	−48 −51

*R = Redby. I = Itasca.

vention of extremely rapid and pronounced temperature changes in the early part of the growing season. Climatic records from the weather station at Redby, on the south shore of Lower Red Lake, indicate that the lake has a noticeable effect on local climate; undoubtedly this effect is even more pronounced on the peninsula itself. When weather data from Redby are compared with those from Itasca State Park, also within the coniferous region but 60 miles to the south, the climate of Redby appears to be milder (Table V). Some of the differences are probably due to the influence of the large lakes, Upper and Lower Red Lake. While it is true that the Itasca weather station is near a lake, Lake Itasca is relatively small, elongate and narrow, nowhere more than one-half mile wide while the Red Lakes are broad and rounded and up to about thirty miles across. Especially noticeable is the effect on late spring and early fall frosts. The latest recorded killing frost at Redby occurred on June 13 and at Itasca Park on June 18; the earliest frost at Redby was recorded on September 4 and at Itasca on August 16. The average date of the last killing frost at Redby is May 23, while at Itasca Park it is May 25. The fall dates are more suggestive. The average date for the first killing frost at Redby is September 25 compared with September 12 at Itasca. Consequently, the average growing season at Redby is 125 days long in contrast to 110 days at Itasca State Park. Thus, it is apparent that the lake acts to extend the growing season and the fall hardening period, and evidently it buffers the spring climate. The slowly melting ice and the cold lake waters probably create a local climate unfavorable to early bud expansion and loss of winter hardness. In this way, losses due to late frosts may be reduced.

The effect of the local climate created by the presence of the lake apparently is limited to the relatively level areas of the peninsula adjacent to the lake. The hills which rise 200 feet or more above the lake level seem to be above the zone where the ameliorating effects are felt. Even the low-lying area in the center of the eastern portion of the peninsula seems beyond the influence of the lake. According to our other criteria this area should be occupied by a deciduous forest, but it supports a spruce-fir community.

The calcareous nature of the drift forming the peninsula must be of considerable importance in maintaining deciduous forests. It has been shown that in some portions of the periphery of their ranges some species may be restricted to calcareous substrata (Oosting 1941 and Salisbury 1952). This may be true for some entire communities. The "Big Woods" west of Minneapolis may be an example. At the northeast border of the "Big Woods" in Minnesota, sugar maple-basswood is limited to calcareous gray drift, while the adjacent non-calcareous red drift is occupied by oak (Daubenmire 1936).

Within the local climatic area, the differentiation of the deciduous forests into distinct communities appears to be determined by subsurface drainage conditions. Sugar maple-basswood occurs on soils with good internal drainage, while mid-gley soils support the basswood-fir-black ash community. Apparently as internal drainage improves, the latter community tends to merge with the former.

Contrary to Kell's (1938) findings at Itasca Park, soil texture did not exercise a major influence over the distribution of maple-basswood. It is found growing on a silty A horizon lying on a friable clay B horizon, in weakly podzolized deep sand and in deep, well-drained gravel. Its occurrence on sand might be explained on the basis of a moderately high water table (5 to 10 feet below the surface) whose effects were not discernible in the three foot soil pit. However, this explanation does not hold, since at two sites maple-basswood was found extending onto deep well-drained gravel, as evidenced by deep gravel pits.

History of the Vegetation

The present composition of the intensively sampled maple-basswood stand gives little hint of its recent history. The complete absence of large birches, bur oaks, or pines, plus the absence of a pronounced podsol of the type that develops under pine-oak stands, indicates that maple-basswood is not a recent invader as it may have been at Itasca Park (Buell and Cantlon 1951). The stand, which is reproducing well in all size classes, has the look of a mature forest that has occupied the area for a long period of time.

The soil underlying the stand lends support to this view. The leached grood or strongly degraded chernozem soil is similar to that found by Buell and Cantlon (1951) under a maple-basswood forest that recently invaded the prairie or brushland near Waubun, Minnesota. This soil, however, differs from the Waubun soil, since the processes of leaching have gone much further. The gray-black crumb structure in the lower A horizon present at Waubun is completely absent in this soil, as is the platy structure in the upper A horizon. This advanced condition of podzolization may be taken as an indication of exceptionally long occupation by deciduous forests. If the slightly degraded chernozem at Waubun dates back 140 years, this strongly degraded chernozem must antedate it by many centuries. This would be expected on the basis of geographical location, since this stand is located approximately 60 miles east of the present prairie border. Consequently, any forest invasion of prairie would have occurred centuries ago when the prairie-forest transition lay farther to the east.

Soils examined elsewhere on the peninsula give little indication of the distant history of the vegetation of the region, but the immature soil under the maple-basswood at the south end of the transect and the poorly developed gley soil under the basswood-fir-black ash suggest an occupancy by stable forest communities more recent than that indicated by the strongly degraded chernozem. There are, however, the alternatives that profile development has been retarded because of deep coarse sands under the maple-basswood and the poor subsurface drainage under the basswood-fir-black ash.

Quadrat data from the basswood-fir-black ash stand show that its composition is changing. Ten tree species are found in the largest diameter class, 8 in the middle diameter class, and only 6 in the smallest diameter class (Table III). The figures on basal area also show striking changes. Basswood, fir, and black ash make up only 37% of the total basal area in the greater than 10 inch d.b.h. class. In the 4-10 inch d.b.h. class they compose 72%, and in the 1-4 inch d.b.h class they show almost complete dominance with 99% of the total basal area in that size class. Since these 3 species are the only ones satisfactorily reproducing, there is little doubt that they will eventually dominate the stand.

This stand was dominated (perhaps 200 years ago) by paper birch, white pine, and bur oak. This is evidenced by scattered large individuals of these species in the upper canopy and by numerous large fallen and decaying birches. This birch-pine-oak community is typical today of the well-drained upland sites. Here it is being replaced by a community typical of swampy places composed of species tolerant of poor internal soil drainage. Black ash is commonly a peat soil species (Kell 1938), while fir is very tolerant of wet soils. Basswood does not appear to be as tolerant of wet places as ash or fir, but it is able to maintain itself under changing conditions, perpetuating itself by sprouts.

What explanation can be given for the earlier establishment of the birch-pine-oak forest and for its displacement by the present community? On the basis of the authors' observations the birch-pine-oak community is thought to be successional, probably resulting from some past disturbance. Cutting in this instance could not have been a factor, since these stands date well before the occurrence of lumbering in this region. Wind throw might have been of importance, but if this area was as poorly drained as it is today it seems improbable that dry site species such as bur oak, white pine, and white birch would have become established following removal of the wet-site species by wind action.

Fire might have been the cause, but if climatic conditions at the time the stand was established were the same as they are today, even this seems unlikely. Since 1864 when the Chippewa migrated to the Point, population pressure has become greater and the chances for fire seem to have increased. Today, man-made fires are not rare on the Point. A Chippewa leader stated that the hilly, sandy portions of the peninsula have been recently burned over on several occasions. However, within the memory of our informant (about 50 years), there has been no serious fire in the well-developed deciduous forest on the lower flanks of the peninsula.

Since fire has been common on the Point but uncommon in the well-developed deciduous forests, it seems that under the existing climate they are not subject to frequent burning. This is in line with our observations, for in the three summers that we have visited the basswood-fir-black ash stand, not once did it seem to be highly inflammable. In fact, in August 1949, there was standing water on the ground.

Climatic change, possibly accompanied by a change in fire incidence, may be the most logical explanation for the vegetation changes. A former, drier climate would have favored a lower water table and less mesic conditions. These conditions, in turn, would have favored fire, and fire could have been responsible for the establishment and maintenance of successional communities; or conceivably communities now successional may have been stable under the different climatic conditions and not dependent upon fire. A shift in climate with an increase in moisture would have resulted in a rising water table, less favorable fire conditions, and the expansion of more mesic communities out of geographical or moist site refugia.

This hypothesis not only fits the Red Lake data well, but it is in agreement with the findings of Buell and Cantlon (1951), as well as with earlier concepts of the history of the vegetation of the middle west (Gleason 1923). Buell and Cantlon concluded that climatic change may have been the principal factor controlling sugar maple-basswood invasion of pine at Itasca Park, and of prairie or "brush prairie" near Waubun, Minnesota.

At the present time, maple-basswood on Ponemah Point is very actively invading cut-over pine land underlain by coarse soils. Stands along the south end of the transect show a regular progression from mature maple-basswood, through mixtures of smaller maple trees with aspen, to a condition where sugar maple seedlings and saplings were found growing in large numbers under aspen cover.

This expansion might be related to more favorable climatic conditions; however, part is probably related to the changing culture of the local Chippewa Indians. Prior to the mid-twenties, the Indians maintained a type of hunting-fishing-gardening economy. In 1925, a permanent sawmill opened. This was followed in 1929, by the inauguration of commercial fishing on the Red Lakes. As these industries developed there was a gradual shift to a wage economy. With increased steady income, the Indians abandoned their gardens and blueberry picking, and turned more and more to canned foods. The almost complete elimination of light burning to increase production of blueberries, and the installation of a fire protection system in conjunction with the forestry program, limited fire as a factor acting against the spread of mesic hardwoods. Additionally, hundreds of acres of pine forests were cut adjacent to the maple-basswood stands. The limitation of fire and the removal of pine competition have almost certainly contributed to the expansion of the maple-basswood on coarse soils.

SUMMARY

Ponemah Point, a calcareous moraine, is a peninsula almost separating Upper and Lower Red Lake. It lies well within the area mapped by Upham as the coniferous region of Minnesota. In this position, its hardwood forests represent a deciduous outpost in a primarily coniferous region.

The lower parts of the peninsula along its north and south sides and at the western end are occupied by hardwood forests. The higher elevations, covered by forests of white and red pine until removed by recent logging operations, are now covered by a forest of paper birch, red maple, and aspen. The low-lying east end supports forests of spruce, fir, and white cedar or successional stands of birch and aspen.

Two distinct types of hardwood forests whose distribution seems to be related to soil drainage are described: a maple-basswood community on the better drained sites, and a basswood-fir-black ash community on the poorly drained sites.

At present, the maple-basswood appears to be a stable community. Its structure shows no evidence of recent change. However, the underlying grood soil is suggestive of an occupancy by prairie in xerothermic time.

The basswood-fir-black ash community shows a changing composition. This community is replacing a forest formerly dominated by paper birch, white pine, and bur oak. This is interpreted as indicative of a climatic shift toward a wetter climate. This shift may have acted directly

through changed soil moisture conditions, or indirectly through decreased fire incidence, or both.

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THE SPIDER POPULATION OF THE ABSTRACT BROOMSEDGE COMMUNITY OF THE SOUTHEASTERN PIEDMONT

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INTRODUCTION

Animal ecologists have made innumerable studies of many different types of communities both from a faunistic and an environmental standpoint, but the vast majority of these studies have been limited to a single or a few stands of the community, *i.e.*, only concrete communities have been studied. However, the ecological community can also be thought of in an abstract sense. These two concepts, the abstract and the concrete community, are not new and have long been used by plant ecologists. A concrete community of oak-hickory, for example, refers to one particular stand at a specific location. On the other hand, and using the same example, one can think of all the stands of oak-hickory in general without particular reference to any one stand. This would be the abstract oak-hickory community.

To the authors' knowledge no studies have been made concerning the animal population of the abstract community. This is difficult to understand in view of the fact that the validity of faunistic studies on concrete stands of various types of communities is based essentially on the supposition that these faunas exist in the abstract community as well. The scope of this investigation, therefore, deals with the question: to what extent do animal populations exist in an abstract sense within the community?

Interest in this problem was aroused while studying the spider populations inhabiting maritime communities on the coast of North Carolina (Barnes 1953). With the exception of the intertidal grass, *Spartina alterniflora,* only single concrete stands of the various communities were studied. Ten widely scattered stands in Spartina were sampled and it was found that the spider population of all stands was essentially the same, *i.e.*, the abstract Spartina community supported an abstract spider population and the variations which existed were no greater than the variations in the vegetation.

The current investigation was carried out to study more fully the animal population of a single abstract community which covered a wide geographical area. Spiders were used as an index of the population because of the familiarity of the authors with their taxonomy and the ease with which they can be quantitatively collected. Broomsedge, Andropogon, was selected since it is abundant in the Southeast and it is easily recognized from a distance while traveling. The investigation was limited to stands of broomsedge in the piedmont of North Carolina, South Carolina, Georgia and Alabama.

The authors wish to express appreciation to the Duke University Research Council for their financial aid in support of this project and also to Dr. W. J. Gertsch of the American Museum for his aid with various taxonomic problems involved in the identification of the spiders.

COMMUNITY

Broomsedge, Andropogon, is one of the most common and conspicuous grasses in the United States and assumes a dominant position in many communities. It is an important member of the prairie climax in the western portion of the United States and forms an intermediate stage in various successional series in the East.

In the piedmont of the Southeast broomsedge is an important member of the secondary successional series of communities. The vegetation of this series has been described by Oosting (1942) and the causal factors have been studied by Keever (1950) and Bormann (1953). If a cultivated field is allowed to go fallow Leptilon, horseweed, will assume a dominant position the first year following abandonment. This is replaced the second year by an aster community. The third year broomsedge appears and maintains a dominance for several years until it is replaced by pine which eventually gives way to the oak-hickory climax.

The duration of the broomsedge community is quite variable and largely determined by the proximity of a seed source for the succeeding pine community. Under favorable conditions pine seedlings may appear during the third year of the broomsedge community, *i.e.*, the fifth year following abandonment. On the other hand, pine in some cases may not appear in any numbers for twenty years.

Andropogon virginicus is the most common species of broomsedge forming this community.

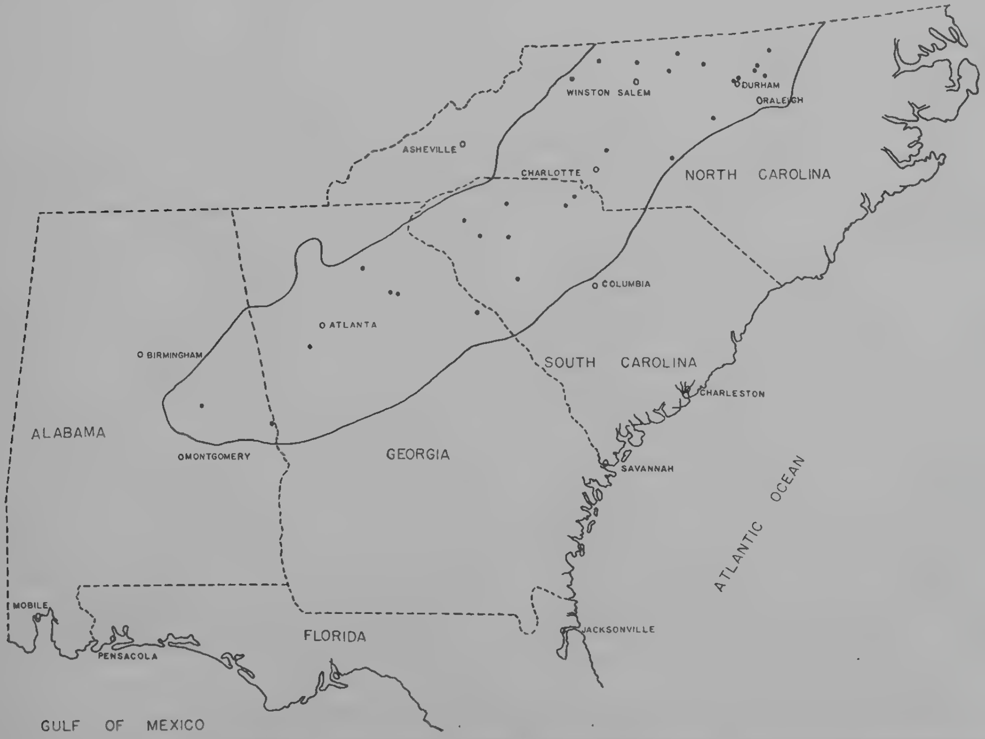

FIG. 1. Map of the southeastern piedmont and location of broomsedge stands (black dots) investigated in this study.

This species usually reaches a height of two and one-half to three feet and forms basal clumps that annually increase in size, thereby creating a relatively uniform and compact cover.

A number of other species of plants, particularly composites, grow between the clumps of broomsedge. While these are common members of the community they are always subordinate to Andropogon. Certain other species are sporadically abundant, trumpet vine, brambles and Bermuda grass being the most conspicuous of these.

METHODS

A total of 29 fields of broomsedge was sampled from June through August of 1953. Sixteen fields were located in North Carolina, six in South Carolina, five in Georgia and two in Alabama (Fig. 1). In addition to these, one field was sampled each month from May through August so that any seasonal variation in the spider population might be ascertained. One stand of aster was sampled for determination of successional variations.

Although broomsedge communities were studied only in one physiographic province, the degree of variation in this communnity due to age of the stand, degree of compactness of the dominant, terrain, etc., is extremely great. For this reason it was impossible to select absolutely uniform stands. Two conditions, however, were met in the selection of any field: the stand had to be larger than ½ acre and Andropogon the only dominant plant.

Vegetational variation in each stand was measured by means of a thirty-foot transect. This provided information as to the abundance of the plants in the field as well as the percentage of compactness of the broomsedge. The latter information was obtained by measuring the distance occupied by broomsedge clumps along the line and dividing this total by the total length of the transect. In addition to this the nature of the bordering vegetation, the prevalence of pine seedlings and isolated young pines, and the age of each field was estimated as closely as possible.

Only the spider population inhabiting the herbaceous level was investigated. The ground fauna was ignored because of the large amount of time required to sample this stratum and it was felt that the time saved could be better utilized in increasing the total number of fields sampled.

Each field was sampled quantitatively by sweeping. For this purpose a sweep net with a diameter of sixteen inches and a handle three feet long was used. Ten separate sample units consisting of 100 strokes each with the net were taken in each field. The second stroke of the net always covered the same arc as the first but was swept in the opposite direction. A single step forward was then taken and two more strokes were made in the same manner. This method lessened the chance of missing the more tenacious species. On completion of the 100-stroke sample unit the contents of the bag were emptied onto a white sheet for examination. The spiders were then separated from the debris and placed in a glass vial containing 70% alcohol.

All spiders collected were identified in the laboratory following completion of the field sampling. The identification of immatures in many cases was made on the basis of the adult species which had been collected. This undoubtedly produced a certain amount of unavoidable error. In certain genera, such as *Xysticus* and *Argiope,* where more than one species were known to occur and the immatures were indistinguishable, the species within the genus were grouped together. A very small percentage of the spiders collected could not be placed beyond family. The majority of this group represented single or isolated species and would therefore have little effect on the over-all population picture of the spiders inhabiting any one stand. These unknowns were, nevertheless, counted in calculating the species and density totals of each field.

All species collected in this study are listed by family in Table I and representatives of all species have been deposited in the collection of the American Museum of Natural History.

Four statistical terms, frequency, density, constancy and presence, were used in expressing the quantitative sampling described above. Frequency, as used in this study, indicates the number of times a particular species occurs in a given number of samples, all of which have been taken in the same concrete community. Density, on the other hand, is the average number of individuals of a species per sample. As an example, if ten samples were taken in a particular field and twenty individuals of species A were collected in the first sample and none in the remaining nine, this species would have a frequency of ten percent and a density of two, i.e., an average of two per sample.

Constancy, like frequency, refers to the number of times a certain species occurs in a given number of samples. It differs from frequency, however, in that each sample is taken from a *different* stand of the abstract community while frequency refers to samples, all of which have been taken in the *same* stand. Thus, constancy bears the same relation to the abstract community as does frequency to the concrete community.

Presence refers merely to the occurrence of a

TABLE I. *List of the spiders collected in the twenty-nine fields of Broomsedge investigated in the piedmont of southeastern United States*

- Theridiidae
  - *Allotheridion differens* (Emerton)
  - *Allotheridion dividuum* (Gertsch and Archer)
  - *Allotheridion murarium* (Emerton)
  - *Allotheridion pennsylvanicum* (Emerton)
  - *Conopistha partita* (Walck.)
  - *Hentziectypus globosus* (Hentz)
  - *Latrodectus mactans* (Fabricius)
  - *Tholocco unimaculata* (Emerton)
  - *Theridula opulenta* (Walck.)
- Linyphiidae
  - *Frontinella pyramitela* (Walck.)
  - *Tapinopa bilineata* (Banks)
  - *Tennesseellum formicum* (Emerton)
- Micryphantidae
  - *Ceraticelus alticeps* (Fox)
  - *Ceraticelus creolus* Chamberlin
  - *Ceraticelus fissiceps* (Cambridge)
  - *Ceratinopsis interpres* (Cambridge)
  - *Eperigone* sp.
  - *Erigone autumnalis* Emerton
  - *Grammonota* sp.
- Epeiridae
  - *Acanthepeira stellata* (Walck.)
  - *Argiope aurantia* Lucas
  - *Argiope trifasciata* (Forskal)
  - *Conepeira atlantis* Archer
  - *Cyclosa turbinata* (Wqlck.)
  - *Eustala anastera* (Walck.)
  - *Kaira alba* (Hentz)
  - *Kaira* sp.
  - *Larinia directa* (Hentz)
  - *Mangora gibberosa* (Hentz)
  - *Metepeira labyrinthea* (Hentz)
  - *Neoscona minima* Camb.
  - *Singa truncata* Banks
  - *Wagneriana tauricornis* (Camb.)
- Tetragnathidae
  - *Mimognatha foxi* (McCook.)
  - *Tetragnatha laboriosa* Hentz
- Mimetidae
  - *Mimetus notius* Chamb.
- Hahniidae
  - *Neoantistea* sp.
- Lycosidae
  - *Geolycosa* sp.
  - *Lycosa rabida* Walck.
- Oxyopidae
  - *Oxyopes salticus* Hentz
  - *Oxyopes scalaris* Hentz
  - *Peucetia abboti* (Walck.)
- Gnaphosidae
  - *Gnaphosa* sp.
  - *Pencilochroa famula* (Chamberlin)
- Clubionidae
  - *Agroeca* sp.
  - *Chiracanthium inclusum* (Hentz)
  - *Clubiona abboti* Koch
  - *Clubiona catawba* Gertsch
- Anyphaenidae
  - *Anyphaenella saltabunda* (Hentz)
  - *Aysha gracilis* (Hentz)
- Thomisidae
  - *Misumena calycina* (Linnaeus)
  - *Misumenoides aleatorius* (Hentz)
  - *Misumenops celer* (Hentz)
  - *Tmarus* sp.
  - *Tibellus duttoni* (Hentz)
  - *Philodromus rufus* Walck.
  - *Philodromus imbecillus* Key
  - *Philodromus* sp.
  - *Philodromus* sp.
  - *Thanatus lycosoides* (Emerton)
  - *Xysticus discursans* Key.
  - *Xysticus ferox* (Hentz)
  - *Xysticus fraternus* Banks
  - *Xysticus luctans* (C. L. Koch)
- Salticidae
  - *Agassa cyanea* (Hentz)
  - *Corythalia deliculata* Gertsch and Mulaik
  - *Gertschia noxiosa* (Hentz)
  - *Habronattus coronatus* (Hentz)
  - *Hyctia pikei* Peckham
  - *Icius* sp.
  - *Maevia* sp.
  - *Metaphidippus protervus* (Walck.)
  - *Neon nellii* Peckham
  - *Onondaga lineata* (Koch)
  - *Paraphidippus pineus* Kaston
  - *Peckhamia picata* (Hentz)
  - *Philippus abboti* Chamberlin and Ivie
  - *Phidippus clarus* Key
  - *Phidippus princeps* (Peckham)
  - *Poultonella alboimmaculata* Peckham
  - *Thiodina puerpera* (Hentz)
  - *Zygoballus sexpunctatus* (Hentz)
- Dictynidae
  - *Dictyna* sp.
  - *Dictyna volucripes* Key.
- Uloboridae
  - *Uloborus americanus* (Walck.)

species in a particular stand without considering its abundance or frequency. When used in relation to the abstract community it is usually expressed as a percentage. As an example, if species A occurred in seven out of ten stands, regardless of whether one or one hundred individuals were represented in any one of the seven stands, this species will have a presence of 70%.

RESULTS

TABLE II. *Summary of the Twenty-Nine Stands of Broomsedge Investigated*

Location	Age Since Cultivation	% Compactness of Broomsedge	Spiders Number of Species	Spiders Number of Individuals	Date Sampled
1. Durham Co., N. C.	8	33	24	211	June 5, 1953
2. Durham Co., N. C.	10	51	24	178	July 25, 1953
3. Granville Co., N. C.	5	56	19	84	June 2, 1953
4. Granville Co., N. C.	4	52	27	158	June 2, 1953
5. Vance Co., N. C.	4-5	46	24	129	June 2, 1953
6. Wake Co., N. C.	5-6	39	25	99	June 2, 1953
7. Guilford Co., N. C.	4-5	44	29	211	June 10, 1953
8. Stokes Co., N. C.	7-8	78	22	142	June 10, 1953
9. Rockingham Co., N. C.	8-10	80	16	122	June 10, 1953
10. Wilkes Co., N. C.	3	48	22	124	June 11, 1953
11. Surrey Co., N. C.	6	35	22	148	June 11, 1953
12. Alamance Co., N. C.	7-8	63	28	196	July 10, 1953
13. Chatham Co., N. C.	8-10	62	22	232	July 30, 1953
14. Montgomery Co., N. C.	5	65	20	161	July 30, 1953
15. Cabarrus Co., N. C.	8	64	28	315	July 30, 1953
16. Greenville Co., S. C.	6	70	25	256	Aug. 3, 1953
17. Pickens Co., S. C.	5-8	35	21	191	Aug. 3, 1953
18. York Co., S. C.	4	56	21	133	Aug. 4, 1953
19. York Co., S. C.	5	50	27	266	Aug. 4, 1953
20. Laurens Co., S. C.	3-5	55	27	255	Aug. 6, 1953
21. Spartenburg Co., S. C.	3-5	37	20	295	Aug. 8, 1953
22. Saluda Co., S. C.	5	60	25	185	Aug. 11, 1953
23. Wilkes Co., Ga.	5-7	51	25	345	Aug. 11, 1953
24. Clark Co., Ga.	3-5	40	21	117	Aug. 11, 1953
25. Clark Co., Ga.	15-20	42	26	257	Aug. 12, 1953
26. Hall Co., Ga.	8-10	74	26	170	Aug. 12, 1953
27. Fulton Co., Ga.	3-5	46	26	248	Aug. 12, 1953
28. Chambers Co., Ala.	3-5	58	23	128	Aug. 13, 1953
29. Tallapoosa Co., Ala.	20	70	21	257	Aug. 13, 1953

A total of 5,615 spiders belonging to 85 different species was collected from the twenty-nine stands of broomsedge sampled during this study. The average number of species per stand was 23 and the average number of individuals was 193. As has been previously stated these figures are based on ten samples per stand. The range of variation in both cases, especially in regard to the number of individuals per field, was relatively great. The number of species per field ranged from 16 to 29 while the total number of individuals ranged from 99 to 345. These data are summarized for each field in Table II.

All attempts to correlate population size and the number of species which a particular field supported proved futile. For example, in many cases fields which maintained a spider population of a relatively low density included a large number of species and in just as many instances the reverse was true. Thus, it was quite obvious that the number of species found in any field was not necessarily a simple function of the population size. All attempts to correlate population size and number of species with other factors such as compactness of the broomsedge dominant, homogeneity of the vegetation, age of stand and time of collection proved futile. In all cases where either population size or species numbers were plotted against any one of the factors mentioned above only random scattering resulted.

Frequency-Density. Of much more importance were the results attained from an analysis of the sampling data as it related to the actual population structure of spiders in broomsedge. From each of the series of ten sample units taken in a field a frequency-density diagram of the spider population of that field was constructed. This method of analysis gave a graphic picture of the spider population structure of each field of broomsedge. A comparison of these diagrams showed them to be very similar, *i.e.*, every field of broomsedge investigated was found to have essentially the same population structure of spiders. This was true not only with regard to the species present but also in regard to the density of the different species. These results are illustrated in Figure 2 where one field, selected at random, from each state is represented. It will be noted immediately that each field displays essentially the same population structure despite the fact that they cover a range of approximately six hundred miles. There is some degree of variation in the densities of certain species but this variation is certainly not large enough to obscure the over-all homogeneity between stands.

It should be remembered that density as used here is absolute, *i.e.*, the actual numbers of each species collected. The scale of density shown at the bottom of the figure indicates the average number per sample. The total number of a particular species collected in the stand can be ascertained by comparing the width of the bar with the scale and multiplying by ten. While the use of relative density might have lessened to some extent the variation between fields the authors felt that by basing the density on the actual numbers collected there was less change of misinterpretation and obscuring the data.

Constancy. Additional indication of the homogeneity of the spider population in broomsedge was shown by compiling the sampling data in terms of constancy. As an example, the seventh sample unit was selected from the ten units taken in each field. The data resulting from this sample in each of the twenty-nine fields were then arranged in terms of frequency-density as was done previously for each individual stand of broomsedge.

The results of this compilation are shown in the constancy-density diagram at the top of Figure 2. The picture derived from this method of handling sampling data is basically the same at that for the individual stands shown in the same figure. This is particulary significant since constancy includes all of the fields surveyed.

The chief difference between the constancy-density and frequency-density diagrams shown in Figure 2 is the reduction of extremes in the former. This would be expected since in one respect a constancy diagram can be thought of as an average of all stands.

In order to test the validity of the constancy

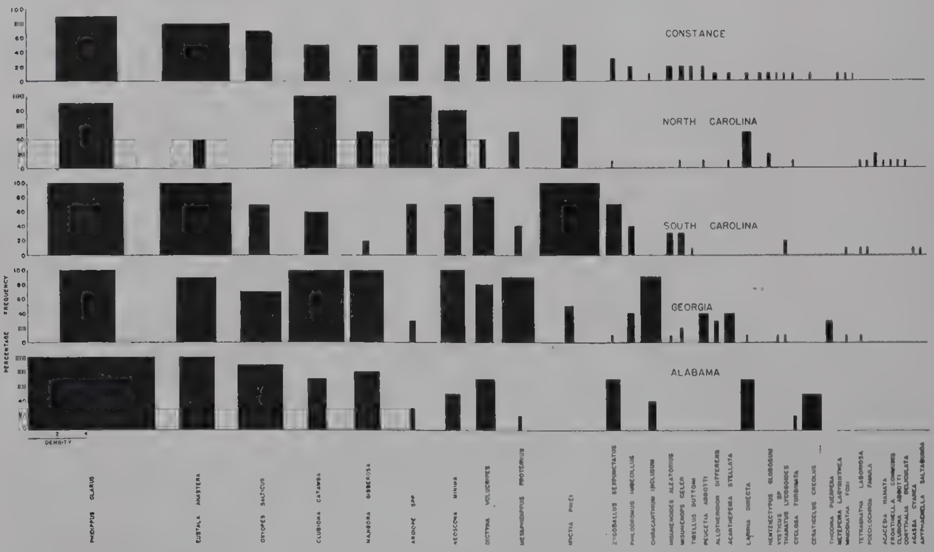

FIG. 2. Constancy-density diagram of the spider population in twenty-nine stands of broomsedge (upper graph); frequency-density diagrams of the spider populations in four different stands of broomsedge (lower graph).

diagram shown in Figure 2 samples other than the seventh from each series were analyzed. The results showed the same pattern with the exception of variations among the rarer species in the community.

Presence. Another approach to the sampling data is shown in Table III where the first fifteen species of spiders in order of percentage of presence and density are tabulated. While only two species, *Phidippus clarus* and *Mangora gibberosa* occurred in every field, eight other species had presence percentages of over 90%.

TABLE III. *Species of spiders with the highest density and percentage of presence in twenty-nine stands of broomsedge*

PRESENCE		DENSITY	
	% Fields in which Species Occurred		Average Number per Field
1. *Phidippus clarus*	100	*Phidippus clarus*	33.8
2. *Mangora gibberosa*	100	*Eustala anastera*	27.2
3. *Argiope* spp.	97	*Mangora gibberosa*	14.0
4. *Eustala anastera*	97	*Oxyopes salticus*	13.8
5. *Metaphidippus protervus*	93	*Hyctia pikei*	12.5
6. *Neoscona minima*	93	*Clubiona catawba*	11.9
7. *Oxyopes salticus*	93	*Neoscona minima*	10.0
8. *Zygoballus sexpunctatus*	93	*Dictyna volucripes*	10.0
9. *Dictyna volucripes*	90	*Argiope* spp.	9.1
10. *Clubiona catawba*	90	*Metaphidippus protervus*	6.1
11. *Chiracanthium inclusum*	86	*Zygoballus sexpunctatus*	5.5
12. *Hyctia pikei*	86	*Philodromus imbecillus*	4.0
13. *Misumenops celer*	79	*Misumenops celer*	3.0
14. *Thiodina puerpera*	69	*Thiodina puerpera*	3.8
15. *Philodromus imbecillus*	69	*Chiracanthium inclusum*	3.3

The significance of this list is best seen by comparing it to the similar ranking of species in order of density in the same table. This list is very similar to that for presence. Of the first five species listed for percentage of presence three of these occupy a similar position in order of density. All except one of the first ten species listed under presence are among the ten species with the greatest density.

The relationship of presence and density in certain species is quite interesting. *Hyctia pikei,* when present, always occurred in great numbers and ranked fifth in order of density; however, it was completely absent from four fields. *Metaphidippus protervus* exhibited the reverse condition —while present in all fields except two, its density was less than half that of *Hyctia pikei.*

Considering only the twenty-five most prevalent species in broomsedge, the hunting forms outnumbered the web spinning forms approximately 3:2. However, when density is considered a more balanced condition as approached with the ratio being about 28:25. This prevalence of hunting forms is probably due to the structure of the vegetation which is less stable for web support than the more rigid shrub and forest communities.

Prior to attempting to correlate the variation in species between different fields with various environmental factors, the sampling data were subjected to a statistical analysis of variance. This was done to determine at the outset if there was a significant amount of variation due to sampling error. For this purpose the data were restricted to the six most prevalent species in broomsedge and ten randomly selected fields in order to keep the computations to a reasonable magnitude. The results of this analysis are summarized in Table IV.

TABLE IV. *Analysis of variance in the sampling data from ten fields and the six most prevalent species in broomsedge. Only the significant* F*-values are given*

Source	Degrees of freedom	Mean square	F
Between fields	9	4.06	
Between samples	9	0.63	
Between species	5	14.16	10.82
Interaction			
Fields x species	45	3.14	2.40
Fields x samples	81	0.58	
Species x samples	45	0.47	
Error	405	1.308	
Total	599		

The analysis indicated that variation due to sampling error was negligible and that the only significant variation was that between the six species and the interaction between species and fields. The high *F*-value between species would be expected and, in part, merely reflects the fact that the population sizes of the six species are not of the same magnitude. This of course is the normal condition occurring in any community.

Seasonal Succession. One field near Durham, North Carolina was sampled each month from May through August in order to determine what, if any, seasonal variation occurred in the spider population of broomsedge during the period of investigation. The results of this series of samples are shown in Figure 3. It can be seen from this diagram that with the exception of early May the spider population remained relatively stable throughout the summer and exhibited little variation. The first series taken in the middle of May showed a low density and frequency peak for almost every species except *Clubiona catawba* and *Phidippus clarus.* Judging from the late-May and early-June samples taken in other stands it seems probable that by the latter part of May the ma-

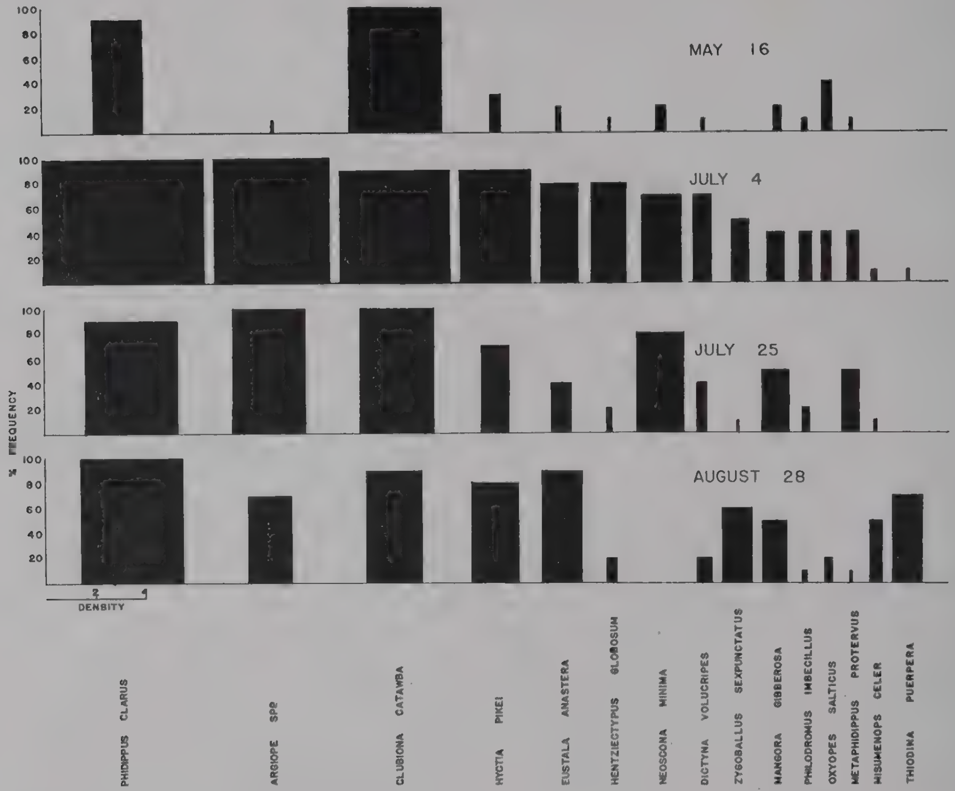

FIG. 3. Frequency-density diagrams of the spider population at different periods in a single stand of broomsedge in Durham Co., N. C.

jority of the important species had reached the normal summer magnitude exhibited during the remainder of the season.

Three species did show a decided population shift, other than the low densities of May, during the summer period. The density of *Hentziectypus globosum* dropped sharply from an early July peak to a very low density during the remainder of the summer. *Neoscona minima* showed a similar shift, reaching a peak during the last of July and then being completely absent from the August collection.

The third species exhibiting a change in density during the summer was *Oxyopes salticus*. This spider was completely absent in May, relatively prominent during the first of July, was rare by the end of the month, and by the end of August its density had risen conspicuously again. The population variation was quite definitely associated with the breeding cycle. The peak shown in the diagram for this species in May represents only adults while the vast majority of the specimens collected during the end of August were juveniles.

Community Succession. In addition to seasonal succession the spider population of the previous aster community in the successional series was also sampled. The following pine community unfortunately was not studied because of the difficulty in sampling quantitatively. If this community were to be sampled it was essential that the stand be at the stage of development where all broomsedge had disappeared. However, when this occurs the young trees are so compact and self-pruning has taken place to such an extent that it would be impossible to take quantitative samples comparable to those taken in broomsedge.

While only one stand of aster was sampled, the results seem to indicate a spider population structure that was to some extent similar to that found in broomsedge. This would seem likely in view of the somewhat open nature and similar growth form of the two communities. The major species in aster were *Metaphidippus protervus, Mangora gibberosa,* and *Misumenops celer* while *Phidippus* *clarus* which had the highest density in broomsedge occurred only once.

Geographical Range. There was relatively little difference in the population picture over the geographical range of the community covered. The major species of the North Carolina stands were also the major species of the Alabama stands. The only forms, the appearance or disappearance of which might be correlated with geographical range, were all relatively rare forms in broomsedge such as the more southern orb-weaver, *Wagneriana tauricornis,* which occurred in Alabama.

Neoantistea, although never abundant, appeared to show some correlation with east-west position of the stands. This species always appeared in fields located along the western edge of the piedmont near the mountains and never in the eastern portion.

Variation in Vegetation. The individual stands of broomsedge exhibited a great deal of variation in the compactness of the dominant grass, Andropogon, as measured by a thirty-foot transect taken in each stand. In some fields the clumps of grass covered as little as 33% of the thirty feet while in others it occupied as much as 80%. No correlation could be obtained between this marked variation in the vegetation and the structure of the spider population. When this factor was plotted graphically against different species-densities of the fields only a random scattering of points resulted.

As mentioned earlier, a number of plant species, *Tacoma radicans, Rubus* and Bermuda grass were sporadically abundant in some of the fields. Again, no distinct correlation could be drawn between this difference in vegetation and the spider population.

Dicussion

The results from the previously shown sampling data indicate quite conclusively that the southeastern broomsedge community supports a definitive and homogenous spider population. This is true not only in regard to the species present but also in regard to their densities within the community. There is thus a characteristic population structure for this group of arthropods that is typical for the broomsedge community. In a graphic sense this structure would be illustrated by the constancy diagram at the top of Figure 2 and the typical species might be said to be: *Phidippus clarus, Eustala anastera, Oxyopes salticus, Clubiona catawba* and *Mangora gibberosa.*

The simplest way to test the validity of the statistical data presented earlier is to conceive of the same type of diagrams constructed from samples of a spider population that were completely random and heterogeneous in distribution. The results would be quite contrasting.

An individual stand might well produce frequency and density diagrams of a similar construction to those shown but there would be little similarity between population diagrams from different stands and constancy structure would consist of a very large number of species with medium size and relatively equal densities, *i.e.,* the curve of constancy and density would be absent or very slight.

It is also conceivable that some ranking of presence might be attained but there would be few extremes and very little correlation with a similar ranking of species by density.

Granting that there is a very high degree of homogeneity in the spider population of broomsedge a logical question might be: to what degree is this population structure distinctive from other community types?

Undoubtedly communities in the same climatic and geographical region with similar types of growth form in the dominant vegetation would support many of the same species of spiders, but the actual constancy-density picture would never be identical. This is corroborated by a previous study (Barnes 1953) in which five different communities in a successional series were analyzed and comparative frequency-density diagrams constructed. An examination of these diagrams indicated the distinctiveness of the population structure of each type.

Although there is a high degree of constancy and homogeneity in the population structure of spiders in broomsedge, some variation does exist between every stand. The problem is not whether it occurs but why, for it could hardly be expected that the populations be exactly the same when no two stands have exactly the same environment. This is true not only in regard to any two stands but at different times within the same stand. The problem of isolating these environmental factors and correlating them with population variations is difficult.

A small percentage of variation can be correlated with seasonal succession. The majority of spiders have a life span of one year and since there is no metamorphosis as in insects, they do not display a great deal of seasonal succession. However, the breeding time varies in different species with resulting gaps or overlaps between adults and spiderlings. Such a gap is displayed by *Oxyopes salticus* in July as was seen in Figure 3. This is usually followed by a preponderance of immatures over adults with a subsequent gradual decrease as the mortality rate takes its toll. This explains the absence of *Oxyopes salticus* in the North Carolina stand in Figure 2, which was sampled in early July, as compared with the high density for this species in the more southern fields which were sampled during the first part of August. The majority of individuals taken in the latter were spiderlings and immatures.

Other factors which were investigated, such as density of the broomsedge dominant, age of stand, prevalence of other vegetation, and geographical location could not be correlated with fluctuations in the densities of the spider population.

This does not mean that these factors are unimportant. They undoubtedly are influents in effecting the population structure of the stand, but are probably operating as an integrated complex with other factors thus making their individual effect difficult to ascertain.

The concept of the abstract community was discussed earlier and it will be remembered that this term refers to the community in general without regard to any particular stand. Thus we can speak of the abstract broomsedge community in the southeastern piedmont. Botanically speaking this represents one of many homogeneous units of vegetation for this climatic and physiographic region which are related to each other in a successional sense.

Any definition of the community must by force consider both plants and animals; however, the concept of the abstract community is rarely applied by animal ecologists because of the lack of investigation of community structure beyond the level of the concrete stand. This to some extent has produced a rather limited outlook in the field of animal synecology. It is believed by the authors that the results of this and previous studies show that the concept of the abstract community can and should be applied to the animal portion of the community as well as to the vegetation. Thus, just as the abstract plant community represents a homogeneous unit of vegetation over a given climatic region, it must also be thought of as including a distinct and homogeneous animal population which is constant and typical for the particular community considered, *i.e.,* abstract animal populations making up a part of the over-all abstract community.

SUMMARY

1. The spider populations of twenty-nine fields of broomsedge were sampled quantitatively in the piedmont of North Carolina, South Carolina, Georgia and Alabama to determine the degree of constancy which an animal population displays in the abstract community. Samples were taken during June, July and early August of 1953 and a total of 5,615 spiders belonging to 85 species was collected during this period.

2. On the basis of frequency-density, constancy-density and presence analyses, all fields of broomsedge were found to maintain essentially the same population structure of spiders both in regard to species present and the relative densities of those species. The abstract broomsedge community can thus be said to support an equally abstract and homogeneous spider population characterized by five major species, *Phidippus clarus, Eustala anastera, Oxyopes salticus, Clubiona catawba* and *Mangora gibberosa.*

3. Although there was a high degree of constancy and homogeneity in the broomsedge spider population, some variation was exhibited by every stand. A portion of the fluctuations of some species could be explained on the basis of seasonal succession.

4. Other possible environmental factors responsible for inter-stand variation were investigated. These factors included the degree of compactness of the broomsedge dominant, prevalence of other vegetation in the stand, character of surrounding vegetation and age of stand. However, no correlations could be made with any of these factors. It is probable that they are important but are operating as an integrated complex which would make their individual effect difficult to isolate.

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ROOT SYSTEMS OF SOME CHAPARRAL PLANTS IN SOUTHERN CALIFORNIA

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Knowledge of the characteristics of plant root systems is important in the management of vegetation for optimum soil stabilization, flood reduction, and usable water yield. Roots bind the soil and anchor the soil mass; the degree of stabilization achieved depends upon the configuration, density, and strength of the root system. Roots absorb water from the soil; the depth to which the soil is tapped for water depends upon the depth to which roots penetrate. Because of these facts, the root sytems of a considerable number of plants have been studied. However, most of the plants studied have been agricultural species (Weaver 1926).

Little is known about the rooting habits of chaparral plants that occupy the steep and rugged mountains of southern California, where erosion rates are high, flood hazard great, and water yield critically important (Sinclair 1954, Sinclair and Hamilton 1953). In the present study, information was obtained about the root systems of the more common chaparral species in these mountains to aid in evaluating the usefulness of the several species for watershed management purposes. The study was carried on in 1951 in the San Gabriel and San Bernardino Mountains.

The topography of the San Gabriel and San Bernardino Mountains is rough, characterized by deeply cut stream channels and slopes that often exceed the angle of repose for soil material. Movement of soil material on most of these slopes is rapid; as a result, there is little evidence of soil profile development.

Soil on the slopes is generally shallow and rocky. The characteristics of the soil are determined largely by the composition of the underlying rock and its susceptibility to weathering (Colman 1948). Here and there, deep deposits of soil material do occur. For example, old stream terraces often have deep clay loam soils with hardpan layers. Sometimes material accumulates at the base of a slope in a deep deposit. On old ridges and in other places where movement is slow because of gentle slope, deep soils have formed in place through long-time weathering of the underlying rock.

Most of the rock underlying the soils is intensively fractured and deeply weathered (Storey 1948). This condition provides opportunity for penetration of roots deep below the soil in many places. Fracturing and weathering is more marked in the metamorphic rocks of the San Gabriel Mountains than in the harder intrusives of the San Gabriel and San Bernardino Ranges.

The climate of the area is Mediterranean. Most of the rainfall occurs in the cool winters. The summers are hot and dry; rainless periods often last 6 months.

The vegetation of the area studied is principally chaparral, although trees grow along the streams and on the shaded sides of the canyons (McMinn 1939). The south-facing slopes are covered principally with chamise chaparrel, and the north-facing slopes with oak chaparral.

The chamise chaparral varies from dense stands of chamise (*Adenostoma fasciculatum* H. & A.) and ceanothus (*Ceanothus* spp.) to open stands of chamise and sage (*Salvia* spp.). Other common species associated with the chamise chaparral are manzanita (*Arctostaphylos* spp.), and small shrubs such as California buckwheat (*Eriogonum fasciculatum* var. *foliolosum* Stokes). Occasionally, the steeper south-facing slopes, and on gentler slopes with gravelly soil, the chamise chaparral gives way to low shrubby vegetation, with California sagebrush (*Artemisia californica* Less.), sages, California buckwheat, yerbasanta (*Eriodictyon* spp.), and deerweed (*Lotus scoparius* (Nutt.) Ottley) as the abundant species. Small-flowered melicgrass (*Melica imperfecta* Trin.) and other herbs are common.

The oak chaparral growing on north-facing slopes is dominated by California scrub oak (*Quercus dumosa* Nutt.). Its commonest associated species are hairy ceanothus (*Ceanothus oliganthus* Nutt.), Christmasberry (*Photinia arbutifolia* (Ait.) Lindl.), birchleaf mountainmahogany (*Cercocarpus betuloides* Nutt.), and occasionally canyon live oak (*Quercus chrysolepis* Liebm.).

The chaparral of the southern California mountains has long been subjected to repeated fires (Jepson 1925). All species are able to reproduce after burning. Some sprout vigorously from the root crowns after the tops have been burned; after repeated fires these root crowns become very large and support many stems. Others are killed by fire, but numerous seeds of these species germinate shortly afterwards and some of the seedlings develop to form part of the returning cover.

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Root systems of only a few chaparral species are described in the literature. These descriptions are, for the most part, based on one individual per species. Plummer (1911) mentioned the large tap root and few laterals present on chamise, which contrasted with the roots of manzanita that ramified in all directions. Cooper (1922) studied root systems of chaparral species near Palo Alto, California. The only mature chamise plant which he investigated did not have a tap root. In contrast, most of the chamise seedings that he excavated did have tap roots. He further noted that chamise, leather oak (*Quercus durata* Jepson), and woolly manzanita (*Arctostaphylos tomentosa* (Pursh) Lindl.) had abundant superficial roots besides many deeply penetrating roots. California yerbasanta (*Eriodictyon californicum* (H. and A.) Torr.) had its main roots in the top 3 inches of soil. Many shoots developed from these lateral roots, but only occasionally did a root grow more deeply into the soil. Jepson (1936) stated that chamise shrubs have strong taproots penetrating downward 3 to 8 feet or more with many strong laterals. He also stated (1939) that the species of manzanitas which do not sprout from the root crown, and which are therefore killed by fire, have shallow roots. Later writers on the chaparral have usually ignored root characteristics or mentioned them only briefly (Sampson 1944).

METHOD OF STUDY

The root systems of chapparal plants were examined at 14 study sites in the San Gabriel and San Bernardino Mountains. At 6 of the sites, roots were exposed by hydraulic excavation. At 8 of the sites, observations were made on the faces of road through-cuts.

The 6 excavation sites in the San Gabriel Mountains were located along road cuts or faces of deep gullies. Plants growing within 3 feet of the edge of the road cut or gully at each site were discarded because of possible alterations in their root systems. Tank trucks equipped with power pumps were used to excavate the soil at these sites. Two types of nozzles were employed—a high pressure, single stream type and a fine spray type. The bulk of the earth around the plant being studied was removed with the high pressure nozzle. Then, to avoid breaking the fine roots, the remaining soil was washed away from the roots with the fine spray nozzle. In this way, an estimate could be made of the number and location of the fine roots.

It was impossible to measure the maximum depth of penetration of roots that disappeared down cracks in the rocks. Therefore, in addition to the sites sued for hydraulic excavation, 8 recently cut roadbanks in the San Gabriel and San Bernardino Mountains were examined for root penetration. No observations were made on root development in the surface layers of soil in these cuts. Only through-cuts were utilized because rooting depths could not be ascertained with sufficient accuracy in hillside cuts. In through-cuts, the shortest distance to the original soil surface could be determined. Where roots could not be traced directly to the proper crown they were identified by their anatomical structure. Unfortunately, some species studied by the hydraulic method were not found growing along the road cuts that were examined.

Information recorded for each site and plant studied included: (1) soil character and depth; (2) size and condition of the plant tops; (3) length, depth of penetration, and radial spread of roots; (4) zones of feeder root concentrations; and (5) other pertinent data such as root grafting and adventitious roots.

DESCRIPTION OF THE SITES

The sites used for hydraulic excavation varied greatly as to soil character and depth. They were all located in the San Gabriel Mountains and were chosen purposely to provide a wide range of soil and vegetation conditions.

An old terrace deposit was excavated at the San Dimas site (2,500 feet elevation). The soil was a clay loam underlain with an impervious hardpan 3 to 5 feet below the surface. This hardpan contained a few cracks through which roots penetrated. The vegetation on this southern exposure was dense chamise chaparral containing many hoary leaf ceanothus (*Ceanothus crassifolius* Torr.) plants and a few black sage (*Salvia mellifera* Greene) shrubs as well as some small-flowered melicgrass. The area had not been burned for 31 years.

At George's Gap (3,600 feet elevation), the soil was a coarse, loose gravel, at least 12 feet deep on a steep east facing slope. The underlying rock was Lowe granodiorite (Miller 1934). The vegetation was open chamise with scattered bigberry manzanita (*Arctostaphylos glauca* Lindl.), chaparral whitethorn (*Ceanothus leucodermis* Greene), and many small shrubs, principally white sage (*Salvia apiana* Jepson), in the openings. The vegetation on this site had not been burned for 54 years.

The soil of the Tie Summit site (5,000 feet elevation) was 2 to 5 feet deep and was underlain with hard but deeply fractured Lowe granodiorite. The top foot of soil was a sandy loam and the rest was decomposed rock becoming harder with depth. The vegetation on this northwestern exposure was low dense chamise chaparral containing chamise, Eastwood manzanita (*Arctostaphylos glandulosa* Eastw.), Mojave Desert ceanothus (*Ceanothus greggii* var. *vestitus* (Greene) McMinn), and an occasional birchleaf mountainmahogany. There was no record of fire within the past 72 years for this site.

The Colby site (3,300 feet elevation) had soil similar to that at Tie Summit, but shallower. The sandy loam soil was only about 6 inches deep. The underlying rock was anorthosite, with the zone of weathering about 2.5 feet deep. The chamise chaparral on this northeastern exposure contained chamise, bigberry manzanita, hoaryleaf ceanothus, and chaparral whitethorn. This vegetation also had been unburned for 72 years.

The soil at the Mt. Lowe site (4,500 feet elevation) consisted of a shallow layer of loose coarse sand, averaging 6 inches deep, over a layer of broken and slightly weathered Lowe granodiorite rock approximately 12 inches thick. The weathered rock was underlain by hard rock with few cracks. The vegetation on this south facing slope was open chamise chaparral containing Eastwood manzanita and chaparral whitethorn. Openings contained California buckwheat and chaparral yucca (*Yucca whipplei* Torr.). Fire had not occurred on this site for 28 years.

The Brown Mountain site (2,500 feet elevation) was on the north side of a rounded ridge of deeply weathered Wilson diorite. The loam to clay loam soil was 2 to 6 feet deep except in spots where weathered rock almost extended to the surface. In contrast to the shallow litter layers occurring at the other excavated sites, the litter and humus on the soil at this site was 3 to 6 inches in depth. Part of the site was covered with a dense growth of chamise and hoaryleaf ceanothus, and part with oak chaparral containing California scrub oak, hairy ceanothus, and Christmasberry. This site burned 16 years previously and was the most recently burned area studied.

Roots of 11 plants were examined on the face of 8 new road cuts. These cuts were located on two major highways in process of construction. Three cuts were on the City Creek road northeast of the city of San Bernardino in the San Bernardino Mountains and 5 were on the Tujunga highway in the western end of the San Gabriel Mountains. The cuts varied from 23 to 50 feet in depth. The materials cut through were either gravel terraces or granitic rock. Some cuts were through hard rock and others through deeply fissured and weathered rock. The vegetation at the road-cut sites on the City Creek highway was chamise chaparral. The vegetation at one road-cut on the Tujunga highway was chamise chaparral, two were in oak chaparral, and two contained species from both types of chaparral.

OBSERVATIONS

The species studied separate into three distinct groups in respect to the general character of their roots (Table I).

1. Woody shrubs with coarse major roots growing downwards: chamise, Eastwood manzanita, chaparral whitethorn, Christmasberry, canyon live oak, and California scrub oak. For these 6 species, depth of downward penetration was greater than radial spread. Chamise and the two species of oak had the greatest penetration (about 25 feet).

2. Woody shrubs with coarse major roots growing laterally: bigberry manzanita, hoaryleaf ceanothus, Mojave Desert ceanothus, hairy ceanothus, and birchleaf mountainmahogany. Radial spread of roots of these 5 species was usually much greater than downward penetration. Hairy ceanothus, though its radial spread was relatively short, had a vertical penetration about equal to other members of this group.

3. Subshrubs with fibrous root ssytems: bush monkeyflower (*Diplacus longiflorus* Nutt.), yerbasanta (*Eriodictyon crassifolium* var. *nigrescens* Brand.), California buckwheat, deerweed, white sage, black sage, and chaparral yucca. These 7 species varied considerably in radial spread but none had roots penetrating more than 5 feet.

The woody shrubs which had their major roots growing downward also had the greatest ability to extend their roots into cracks in unweathered rock. Roots of the first group of species penetrated 2 feet or more into the fine cracks in the hard rock material of the Tie Summit, Colby, Mt. Lowe, and Brown Mountain sites. Because of the hardness of the rock at these sites, the roots were not excavated to their full depth (Table I).

Roots of species in the second group penetrated only short distances, less than 2 feet, into the fine cracks in unweathered rock which were readily penetrated by species of the first group. Roots of the second group could always be traced to their full depth. Roots of species with fibrous systems did not always grow to the full depth of

TABLE I. *Growth characteristics of the chaparral species*

Species	Number of plants†	Average height†	Maximum length of roots†	Maximum vertical depth of root penetration		Maximum radial spread of roots†	Average maximum radial spread		Root/top‡
				Hydraulic sites	Road-cuts		Roots†	Tops†	
		Feet	*Feet*	*Feet*	*Feet*	*Feet*	*Feet*	*Feet*	*Ratio*
Woody shrubs with major roots growing downwards									
Chamise	13	4.9	16.0	8.0*	25.0	12.0*	5.5	2.8	2.0
Eastwood manzanita	4	2.3	13.5	9.0*	17.0	9.0	5.2	1.8	2.9
Chaparral whitethorn	4	4.8	21.0	12.0*	12.0	10.0	8.4	3.6	2.3
Christmasberry	1	4.0	7.0	6.5*	....	5.0	5.0	2.5	2.0
Canyon live oak	..	...	...	...	24.0	...	...	...	...
California scrub oak	3	5.0	15.0	8.0*	28.0	10.0	6.3	2.5	2.5
Woody shrubs with major roots growing laterally									
Bigberry manzanita	4	6.6	31.0*	8.5	...	21.0*	12.5	3.6	3.5
Hoaryleaf ceanothus	7	6.6	14.0	4.5	...	10.0	7.3	2.7	2.7
Mojave Desert ceanothus	2	2.5	13.0	4.5	...	11.0	9.8	1.6	6.1
Hairy ceanothus	3	7.0	8.0	6.0	...	5.5	4.2	2.6	1.6
Birchleaf mountain-mahogany	2	5.0	12.3	5.0	...	9.0	8.5	3.3	2.6
Subshrubs with fibrous roots									
Bush monkeyflower	2	1.3	3.5	2.5	...	3.0	2.5	0.6	4.2
Thickleaf yerbasanta	1	3.0	...	4.5	...	...	...⁑	...	...
California buckwheat	4	1.3	8.0	4.0	...	5.0	3.6	1.3	2.8
Deerweed	2	1.0	5.0	3.7	...	3.0	1.8	1.0	1.8
White sage	1	2.0	9.0	5.0	...	6.0	6.0	2.0	3.0
Black sage	2	3.8	7.0	2.0	...	6.0	5.0	2.3	2.2
Chaparral yucca	2	1.9	13.0	2.5	...	11.0	11.0	2.5	4.4

*Indicates that the deepest or longest root extended farther than recorded.
†Data given only for the plants growing on sites used for hydraulic excavation.
‡Ratio of average maximum radial spreads. ⁑Root sprouts.

the soil and rarely penetrated even short distances into cracks in unweathered rock.

The characteristic rooting habit of each species often was modified by the hardness of the substratum. If the soil was shallower than the usual depth of root penetration and the underlying rock was not sufficiently weathered to permit passage of roots, a layer of roots usually grew on the soil-bedrock interface, the roots entering any cracks present. Roots growing in rock cracks were usually compressed, and feeder roots often formed a mat which filled the cracks. Over the years, organic material had accumulated in the cracks, thus increasing the moisture and nutrients available to the roots.

Roots frequently changed direction, probably in response to hard soil or some other obstacle in their path. Occasionally, roots grew in one direction for several feet only to turn back. One chamise root extended downward for 2 feet, reversed direction, grew upward to within a few inches of the surface and less than a foot from where it had started, and then grew horizontally to become a major lateral root.

On steep slopes, roots were commonly found growing up the slope. These roots often remained at a fixed depth from the soil surface.

Root grafting between individuals of the same species was found only in California scrub oak. No root grafting between different species was found, even though, plants of several species were growing with root sytems so interlocked that they could not be separated intact.

The root crowns of sprouting species were greatly thickened if the tops had been repeatedly removed by fire or other causes. These thickened crowns had been the source of both new shoots and roots.

Nodules were observed on all species of ceanothus. These nodules were similar to those described by Jepson (1936). Van Rensselaer and McMinn (1942) reported that nodules occur on the roots of some species of ceanothus in great abundance but that they do not appear to harbor nitrogen-fixing bacteria. Kittridge (1948) indicated that the nodules might be nitrogen-fixing.

The roots of all species extended laterally much farther than the aerial branches, usually 2 or more times as far, irrespective of the type of root system (Table I). This is in agreement with Weaver and Clements (1938) who stated, "In the majority of both native and cultivated species the root systems are, in proportion to the tops, deeply penetrating and very extensive." Rogers (1935) and Garin (1942) observed that roots of various orchard and forest trees would occupy the entire soil mass between trees even though the trees were widely spaced. For several of the chaparral species, the large root-top ratio may possibly be caused by the shallowness of the soil. These were indications that the root spread of the deep-rooted species and some of the shallow-rooted species varied inversely with the depth of penetration.

Description of Root Systems

The root systems of all species studied have

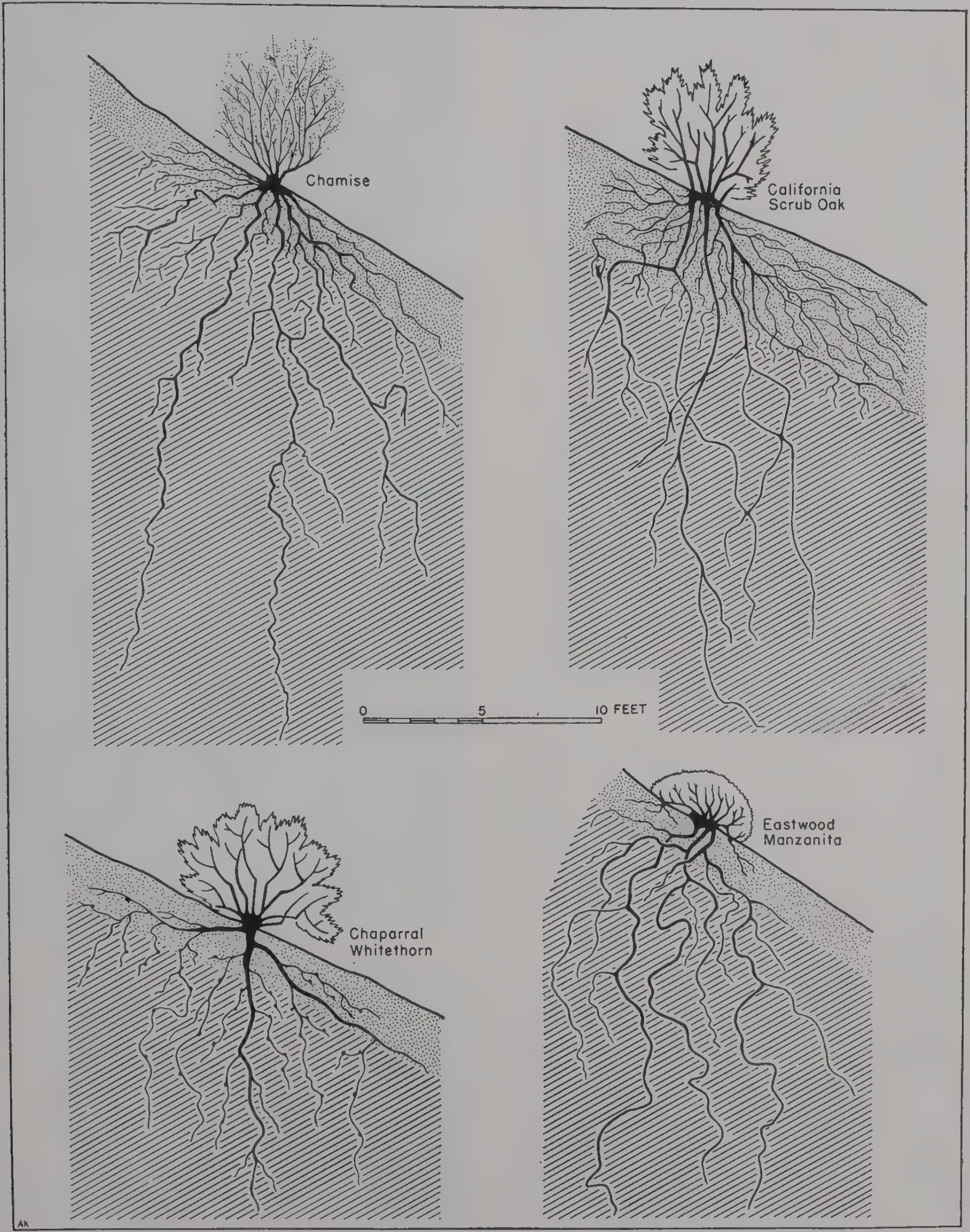

Fig. 1. Diagrammatic sketch of typical root systems of woody shrubs with deeply penetrating roots.

distinctive characters. The features of each species are discussed separately. The species are considered in the same order as their appearance in the tables.

CHAMISE (*Adenostoma fasciculatum* H. & A.)—Chamise is a shrub that sprouts readily from the root crown after fire or cutting. Its root system was generally found to be deeply penetrating, but the roots were of small diameter (Fig. 1). An occasional root was as thick as 1.5 inches, but most main roots were less than 1 inch in diameter. Fine roots were observed in tiny cracks in unweathered rock 25 feet below the surface. Some individuals had a single, deeply penetrating root growing downward from the root crown, but usually several large roots penetrated deeply. Laterals developed from the enlarged root crown, and horizontal branches grew from the main roots. Usually these branch roots grew horizontally for only a short distance and then began to turn downward. The roots were much twisted and changed direction frequently as they grew.

EASTWOOD MANZANITA (*Arctostaphylos glandulosa* Eastw.).—Eastwood manzanita is a shrub sprouting readily from an enlarged root crown. The root systems excavated were similar to roots of chamise (Figs. 1 and 2), though somewhat thicker (up to 3.0 inches in diameter) and more frequently branched. One individual had a single large lateral root which followed the rock surface below-ground for more than 8 feet. In road cuts, roots were observed to a depth of 17 feet. Roots of this species seemed able to penetrate into rock cracks too fine for roots of chamise. Adventitious roots occasionally developed from branches in contact with the ground.

CHAPARRAL WHITETHORN (*Ceanothus leucodermis* Greene).—This ceanothus is a shrub which sprouts readily from the root crown. The specimens excavated had sparsely branched, deeply penetrating root systems. This plant differed from most of the other chaparral species in having a prominent tap root which extended 12 feet or more into gravel deposits or into rock crevices (Fig. 1).

CHRISTMASBERRY (*Photinia arbutifolia* (Ait.) Lindl.).—Christmasberry is a large vigorously sprouting shrub, 10 to 15 feet high, at maturity. One shrub of this species only 2.5 feet high was excavated at the Brown Mountain site. Its root system was much-branched, with many roots about 0.4 inch in diameter growing down and laterally from the root crown. Many roots extended deeper into cracks in unweathered rock than it was possible to excavate. Feeder roots were abundant in the surface humus layer around the base of the shrub and elsewhere throughout the root system. Though this species did not occur on the road cuts that were observed, the one specimen indicated that the shrub would produce deeply penetrating roots at maturity.

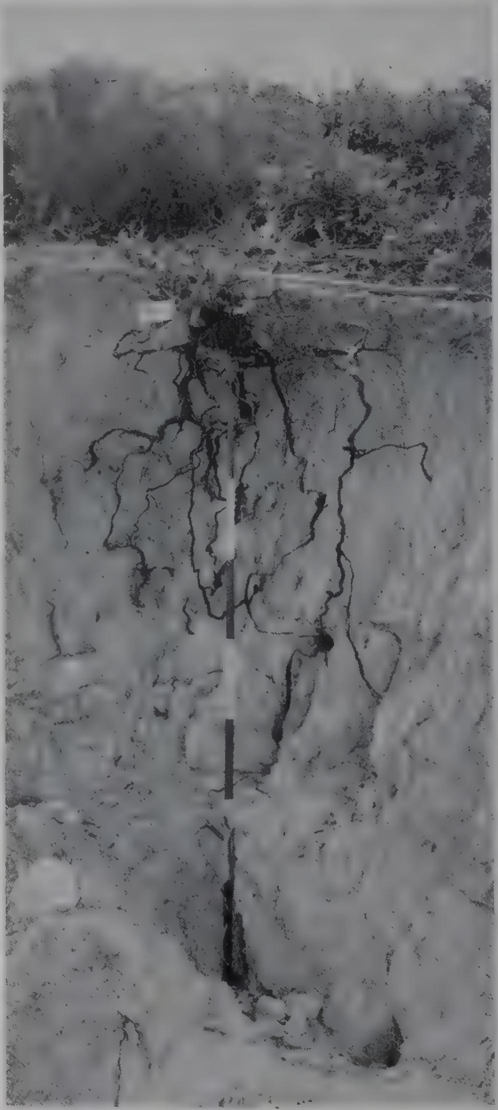
FIG. 2. The roots of this Eastwood manzanita growing at the Tie Summit site had penetrated more than 9 feet of a fine crack in hard rock. At that depth the root was still 0.4 inch in diameter. Note the enlarged root crown and the well-branched root system. (R-82)

CANYON LIVE OAK (*Quercus chrysolepis*

Liebm.).—This tree species was observed only on road cuts, where roots were found at a maximum depth of 24 feet below the ground surface in fractured rock.

California scrub oak (*Quercus dumosa* Nutt.)—The root system of this sprouting species was extensive and contained many branches up to 3 inches in diameter (Fig. 1). These large roots were somewhat contorted and usually angled downward. California scrub oak had the deepest root penetration of all species observed; roots of one shrub grew through fractured rock to a depth of 28 feet below the ground surface. Many fine branch roots grew in all directions from the main roots, but few feeder roots were found in the top 6 inches of soil. This was the only species in which root-grafting was observed.

Bigberry manzanita (*Arctostaphylos glauca* Lindl.).—The major roots of this nonsprouting species were large laterals (up to 3 inches in diameter at the crown) radiating in all directions in the top 2 feet of soil (Figs. 3, 4, and 5). One shrub had a lateral root ½ inch thick 31 feet (root length) from the root crown where it disappeared into a crack in rock too hard for excavation. Even in deep gravel, the roots were largely confined to the top 2 feet of soil, though a few roots penetrated 8.5 feet deep. In shallow soils, there was little penetration of roots into fractured or weathered rock. This species seems to have little ability to send roots into rock crevices which chamise and Eastwood manzanita penetrate readily.

Hoaryleaf ceanothus (*Ceanothus crassifolius* Torr.).—The root system of this nonsprouting species was shallow and composed of many laterally spreading roots, 0.5 inch or less in diameter (Fig. 3). The larger roots were usually sparsely branched but many fine feeder roots grew from roots of all sizes. At the San Dimas site, roots did not penetrate the hardpan, though cracks in this layer were penetrated by chamise roots. Also, hoaryleaf ceanothus roots were not found in fine cracks in unweathered rock readily penetrated by other species. If cracks in the rock contained considerable weathered material, the roots did penetrate. This species of ceanothus was not excavated in deep soil but the individual at the Brown Mountain site showed the greatest unrestricted development. The stem of this plant merged into a rapidly tapering carrot-shaped taproot, 4.0 inches thick at the ground line and 0.5 inch thick at a foot in depth. At this depth, the root behaved as a lateral and grew in an almost horizontal direction. Maximum depth of root penetration of this individual was 4.5 feet and maximum root spread was 4.0 feet. Other shrubs of this species growing in soils 2 feet deep or less and underlain by unfractured rock often had a horizontal spread as great as 10 feet.

Mojave Desert ceanothus (*Ceanothus greggii* var. *vestitus* Greene).—The 2 specimens of this nonsprouting species that were excavated at the Tie Summit site had roots similar to hoaryleaf ceanothus except that the spread of the root systems was somewhat greater.

Hairy ceanothus (*Ceanothus oliganthus* Nutt.).—This ceanothus also is a nonsprouting shrub. The root systems of 3 hairy ceanothus plants excavated at the Brown Mountain site had prominent tap roots and many well-branched but relatively short laterals (Fig. 3). These root systems were shorter than those of all of the other woody species. Maximum length of roots measured from the base of the plant was never more than 6 feet in any direction. The roots were not observed growing into rock cracks. The uppermost lateral roots grew in the top inch of soil.

Birchleaf mountainmahogany (*Cercocarpus betuloides* Nutt.).—The two individuals of mountainmahogany excavated at the Tie Summit site were comparatively small, probably young, plants growing in shallow soil over relatively unfractured rock. The root systems were sparsely branched, widely spreading, and confined mainly to the shallow soil layer and the few rock crevices. The excavation of these shrubs did not give any information as to the comparative ability of roots of this species to penetrate rock crevices, because the shrubs were growing alone.

Bush monkeyflower (*Diplacus longiflorus* Nutt.).—The much-branched, shallow, fibrous root system of this subshrub extended downward a maximum of only 3 feet even where the soil was considerably deeper (Fig. 3). Most feeder roots were concentrated in the surface 3 inches of soil.

Thickleaf yerbasanta (*Eriodictyon crassifolium* var. *nigrescens* Brand.).—The only specimen of this subshrub excavated was growing in deep gravel at the George's Gap site. The main roots followed the slope in all directions about 1 foot below the surface. Only occasionally did a branch root grow deeper even though the soil presented no barrier to root development. These roots were excavated for a maximum distance of 7 feet from the center of the plant, though they apparently went much farther. Numerous stems sprouted from the shallow roots and spread the plant laterally for considerable distances.

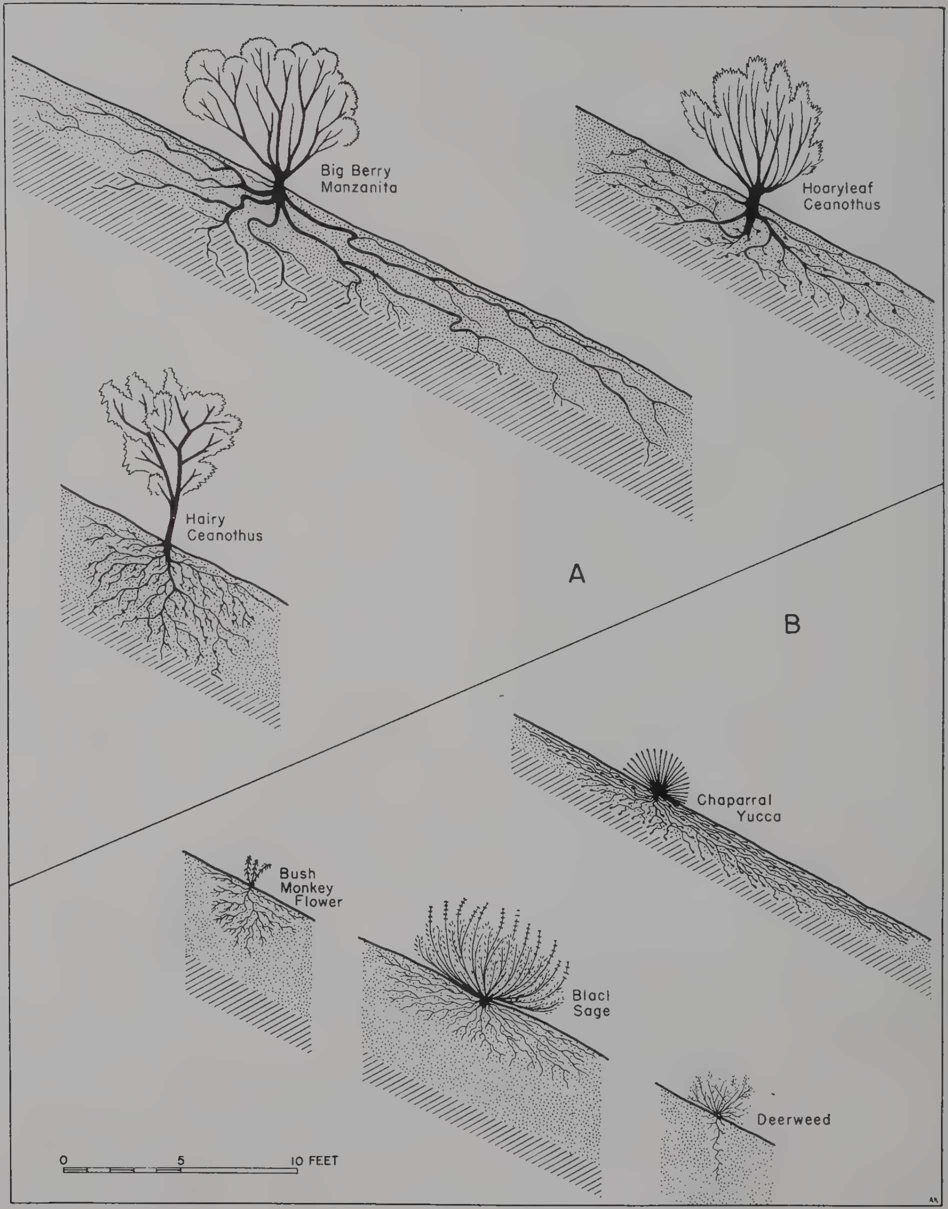

Fig. 3. Diagrammatic sketch of the root systems of, A, woody shrubs with shallow roots and, B, subshrubs with fibrous roots.

California buckwheat (*Eriogonum fasciculatum* var. *foliolosum* Stokes.).—This subshrub had a fibrous much-branched root system, with very brittle roots that were rarely over 0.5 inch, and usually less than 0.3 inch, in diameter. In the deep soil at the George's Gap site, the roots penetrated 4 feet and extended laterally only 2.5 feet. Other specimens growing in very shallow soils at the Mt. Lowe site had the bulk of their roots just above the soil-rock interface and extending laterally a maximum of 5 feet. One plant had its entire root system in a 6-inch layer of soil and broken rock fragments which were underlain by unfractured rock. Adventitious roots developed from branches lying on the ground.

DEERWEED (*Lotus scoparious* (Nutt.) Ottley).—The 2 plants of deerweed excavated at the Brown Mountain site differed from the other subshrubs in having clearly defined taproots (Fig. 3). Inasmuch as the maximum diameter of these taproots was only 0.3 inches and the laterals even smaller, this species is grouped with the fibrous-rooted subshrubs. One plant had a taproot extending straight down for 3.7 feet, with laterals about 6 inches long. The other had a taproot extending down 2 feet to a hard layer in the soil and then horizontally for 3 feet. On this plant, the laterals were less than 6 inches long. No nodulation was observed on the roots of this legume.

WHITE SAGE (*Salvia apiana* Jepson).—The single specimen of this sub-shrub studied had developed a shallow root system in the deep gravel at the George's Gap site. The largest lateral root, 9 feet long, grew slightly uphill and at its terminus was a depth of 5 feet from the surface. This was the plant's greatest depth of penetration. Though the majority of the feeder roots grew from the rootcrown, many developed from the large roots and were concentrated in the upper foot of soil. Adventitious roots grew from stems lying on the ground.

BLACK SAGE (*Salvia mellifera* Greene).—The root system of this subshrub closely resembled that of white sage except that the black sage roots did not penetrate as deeply (Fig. 3). The deepest root excavated was 2 feet below the surface in soil 3 feet deep. The greatest concentration of roots was in the top 5 inches of soil.

CHAPARRAL YUCCA (*Yucca whipplei* Torr.).—This species had a spreading fibrous root system with most roots concentrated in the upper foot of soil (Fig. 3). No roots were observed to penetrate downward more than 2.5 feet. Approximately an equal number of roots grew in all lateral directions from the plant but those growing downhill extended 11 feet while those growing uphill extended less than 6 feet. The root tips averaged 0.2 inch in diameter; the older portions of the roots were only half as thick.

DISCUSSION

The species of plants which make up the southern California chaparral vary in the character of their root systems. The maximum root variability that can occur within any one species probably was not observed because of the shallowness of the soil and the relatively few plants per species studied. However, comparing the different species, the roots exhibited marked differences in depth of penetration, lateral spread, number and size of main and branch roots, and penetration into fractured rock.

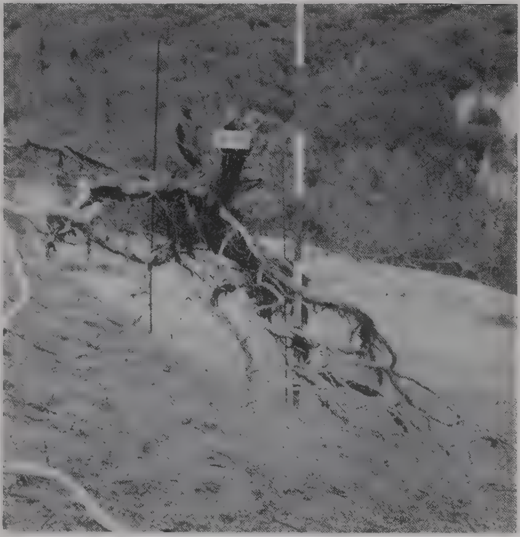

FIG. 4. This bigberry manzanita root system at the Colby site illustrates the characteristic development of a strong surface system. Note the lack of deeply penetrating roots. (R-114)

Species which develop root systems that penetrate deeply (more than 10 feet) into fractured rock structures are Eastwood manzanita, California scrub oak, canyon live oak, and probably Christmasberry. Their root systems are strong, much-branched, and fairly wide-spreading. Chamise has a similar deeply penetrating system but the roots are smaller. Chaparral whitethorn differs in usually having a single taproot instead of the much-branched systems of the other species. All 6 of these species sprout vigorously from the rootcrowns after fire.

Bigberry manzanita is the best example of a widely spread, shallow root system (less than 10 feet). Hoaryleaf and Mojave Desert ceanothus have similar shallow root systems, but neither species spreads as widely as the bigberry manzanita. Hairy ceanothus has a root system somewhat similar in shape to other members of this group, but its roots apparently neither spread as widely nor penetrate as deeply. All of these species are nonsprouters. The sprouting mountainmahogany appears to have a spreading, shallow root system, but the 2 small plants excavated may not have given a reliable indication of the penetration of mature root systems.

The subshrubs, California buckwheat, white sage, and black sage, have much-branched fibrous root systems. Bush monkeyflower has a similar but smaller root system. Deerweed has a slender taproot with comparatively few branch roots. Yucca has shallow but widely spreading roots. Buckwheat and white sage form adventitious roots along the prostrate stems.

Thickleaf yerbasanta has a strikingly different root system. It has widely spreading lateral roots which frequently send up a shoot to form a new plant. This method of propagation often extends the plant over a wide area.

These differences in root systems have important implications in watershed management. On some areas, an increase or other change in the vegetation may bring about benefits such as greater soil stabilization, increased flood regulation, or improved water yield. If manipulation of vegetation is intended, then knowledge of the root systems allows selection of species best adapted to the objectives of management.

Soil stability implications

Plants with roots that penetrate deeply through the soil mantle and into cracks in the underlying rock tend to reduce the mass slumping of material, especially the type of movement originating at a soil-rock interface. Plants with widespreading roots tend to hold surface soil layers in place, but species with only surface roots do not bind the soil as effectively to the underlying rock as those with deeply penetrating roots.

On slopes where the mass movement of soil is to be reduced, Eastwood manzanita, the oaks, and Christmasberry would be desirable species. These species because of their very deep and strong root systems are especially valuable for planting on road fills to reduce the possibility of mass movement. Chamise and chaparral whitethorn are somewhat less desirable because of their smaller or less-branched root systems.

On slopes where soil may be eroded by surface runoff or where surface soil may creep or slide during the dry season, the most desirable plants are those which furnish a continuous cover (Anderson 1949) and grow closely spaced. Those plants which spread laterally by sprouts from shallow roots or by adventitious roots developing from decumbent stems are especially desirable. The subshrubs, California buckwheat, white sage, and thickleaf yerbasanta are in this category, and therefore appear to be the most valuable to reduce this kind of soil movement. However, these species as well as other natives have a high ratio of root-to-top spread, and do not form a continuous cover on south slopes. The high ratio indicates that there is considerable competition between plants for moisture and nutrients and also suggests a possible reason for the sparseness of the native cover (Hellmers, Bonner, and Kelleher 1955).

On some sites, such as road fills, both surface erosion and mass movement may occur. There planting would be recommended using a mixture of deep-rooted woody shrubs and fibrous-rooted spreading subshrubs.

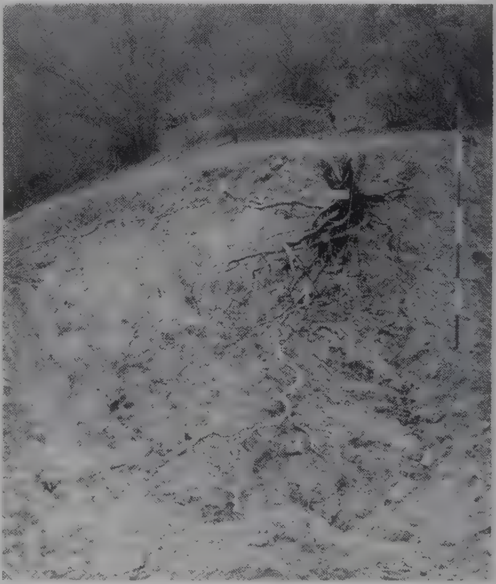

FIG. 5. The same shrub as illustrated in Figure 4. Two large laterals are shown radiating from the root crown. One of these extended more than 21 feet from the base of the shrub and measured 31 feet in length. (R-111)

Water flow implications

Plants with deep roots utilize water from deeper soil and rock layers than plants with shallow roots. This fact is of importance in the management of watersheds both for water yield and for flood control. In the southern California mountains, most of the available water within the root zone is removed by evapo-transpiration during the summer. The moisture content within the root zone must be brought to field capacity by winter rainfall before water is available for entry into the rock structures below the root zone (Kramer 1952, Rowe and Colman 1951).

Where soils are deep, deeply rooting plants make a greater summer drain on soil moisture than shallow-rooting plants. There replacement of vegetation with deep roots by vegetation with shallow roots increases the quantity of water percolating through the soil and thence into streams. In shallow soils, where roots of both shallow- and deep-rooted plants penetrate to the underlying rock, either type of plant uses all available soil water. Where the soil is shallow but the rock cracks can be deeply penetrated by roots, there can be only a small difference in water yield whether deep or shallow rooted species occupy the area. This is due to the fact that the amount of available water held in the rock is quite small in southern California watersheds. Rowe and Colman (1951) reported that in a typical area of the San Gabriel Mountains fractured metamorphic rock below the soil profile could hold no more than 0.05 inch of water available for plant growth, per foot of rock depth.

To increase water yield where mass movement of soil is not probable and where soil is deep, the woody shrubs with shallow, spreading root systems, or the subshrubs, are desirable species to favor in watershed management. Shrubs recommended for this use are bigberry manzanita, hoaryleaf ceanothus, and Mojave Desert ceanothus. They and the subshrubs do not dry the soil as deeply as do the deep-rooted species, and therefore bring about some saving in water. In areas with shallow soil and underlying rock impervious to root penetration, use of water would be much the same regardless of the type of shrubby vegetation.

The deeper drying of the soil-rock mantle by deep-rooted species has another implication for consideration in watershed management. In southern California, some major floods are caused by heavy rains falling upon watersheds whose soil is wet through. Much of the excess water enters the stream as subsurface flow rather than as surface runoff (Lassen, Lull, and Frank 1952). The depth of root penetration influences the amount of space available to store water in the soil at the start of the rainy season. Increased water-storage space made available by removal of soil water by deeply penetrating roots can reduce flood flows during storms, especially if the storms occur early in the season before the soil-rock mantle is wet through. In shallow soils, where roots of both shallow- and deep-rooted species penetrate to the rock, there is no difference in available storage space between the two types of root systems.

SUMMARY

A study was made of the roots of 18 species of shrubs and subshrubs found in the chaparral of southern California. Measurements and observations made on 68 plants at 14 locations in the San Gabriel and San Bernardino Mountains showed the following:

1. Chaparral species and their root systems can be placed into three categories: (a) woody, usually sprouting shrubs with deep-penetrating and wide-spreading systems; (b) woody, usually nonsprouting shrubs with shallow but wide-spreading systems; and (c) subshrubs with shallow, fibrous systems.
2. Roots of some species grew through fractures in the rock or through weathered rock to a depth of at least 28 feet. Subterranean rock crevices were often filled with a mat of living roots.
3. The depth of soil and the extent to which the underlying rock is weathered and fractured modified the characteristics of the root systems.
4. The roots spread wider than the branches in all species studied.
5. Roots of many species grew up hill, parallel to the soil surface.
6. Root grafting was not common. It was found only in one species in this study, California scrub oak.
7. Nodules were found on the roots of all species of Ceanothus.

These findings have important implications for vegetation treatment in watershed management. Species with deep root systems are to be favored for stabilization of the soil mass. Subshrubs which can grow closely spaced, and especially those species which root from decumbent stems or sprout from shallow roots, are useful for reduction of surface soil movement. To reduce some flood flows deep-rooted species should be used on deep soils. To increase water yield on deep soil areas not susceptible to overland water flow, shallow-rooted species should be favored.

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A FIELD STUDY OF THE ACTIVITY OF THE MOLE (*TALPA EUROPAEA*)

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Little is know about the activity pattern of the mole (*Talpa europaea* L.) but it is generally believed to be active during both day and night. Some workers (*e.g.*, Kuzyakin 1935) report greater activity by night than by day, while others (*e.g.* Stein 1950) maintain that there is no difference between the amounts of night and day activity. The frequency of the active periods is unknown although there is a widespread belief among mole-catchers that digging occurs every four hours.

Previous work on the activity of small mammals has been carried out either under laboratory conditions or in the field using indirect methods. The activity of moles has not been investigated in the laboratory, and the only field study is that of Hamilton (1939) who observed the rate of reopening of tunnels in *Parascalops breweri*.

This paper describes an attempt to obtain direct information about the activity pattern of *Talpa europaea* by labelling individuals with radioactive material and locating them at frequent intervals with a Geiger-Müller counter unit.

Material and Methods

Moles were studied in two different habitats.

1. *Pasture* (part of New Fen) at Lakenheath, Suffolk. New Fen, which forms part of the extensive East Anglian fenland, was first cultivated in 1940. It is drained by a series of ditches which cut it up into fields of about ten acres in size. The soil is typical fen peat, with a high humus content. Moles are abundant on New Fen but intensive trapping is confined to the banks of the main drain; elsewhere the animals merely suffer from the effects of agricultural practice. The fields were reseeded in 1947, following severe flooding, and since then have been used only for grazing.

Two females and one male were observed during March and April 1954. Breeding was just beginning, and by the end of this period one of the females was known to be pregnant.

2. *Arable fields* (part of Higham Estate) near Newmarket, Suffolk. The fields used are on light, sandy soil with a low humus content. They were ploughed in May and sown with a mixture of chicory, cocksfoot grass and white clover. The observations were made during the six weeks following sowing, before the crop had grown sufficiently to obscure the moles' shallow tunnels.

Five individuals were studied: one adult female and four juvenile males. Breeding had finished, and the female was in anoestrous condition. The juveniles were sexually immature but had almost reached adult body weight.

Each individual was labelled with 80 microcuries of Cobalt 60. This was contained in a metal ring similar to that used for *Microtus* (1954a, b) but fitted around the base of the tail instead of around the hind leg. (Each ring was made from a monel metal strip measuring 14 mm. x 3 mm. x 0.25 mm.) The use of leg-rings for moles proved to be impracticable because of the shape of the legs; Pavlinin (1948) reports a similar difficulty. The rings remained on the animals for 2-3 months and the virtual absence of predation enabled the majority to be recovered.

The Geiger-Müller counter unit which was used for locating the moles has already been described (Godfrey *loc. cit.*). The G-M probe was remounted at the end of an 8-foot bamboo so that the animals could be located at least ten feet from the observer. With a source of 80 microcuries, it was possible to detect them up to one foot below ground, though in fact they were generally found within a few inches of the surface. The procedure adopted was to study one individual continuously for an 8-hour period. The animal would normally be located at intervals of 3-4 minutes throughout the 8 hours, but recordings were made more frequently if it was moving about. Numbered wooden pegs were used to mark the places where it was found. The behaviour of the individuals clearly showed that they were undisturbed by the work. While feeding, moles often emerged from the ground within a few feet of the observer, and it is evident that they are less sensitive to vibration than is commonly believed.

The 8-hour observation periods were divided into 48 ten-minute units, and the 3-4 recordings which were obtained in each 10-minute unit formed the basis for analysis. There was not sufficient regularity in the records to enable a smaller unit to be used. If an individual was recorded in more than one position within a 10-minute unit it was assumed to have been active for the whole unit, while if it was in the same position at each recording it was considered to have been resting for the whole unit. This method of scoring will tend to underestimate the time spent in rest and overestimate the time spent in activity since rest periods of less than ten minutes will be included within active periods. On the other hand, such activities as eating and grooming, which do not necessarily involve a change of position may be included within rest periods. Digging could readily be observed, and this form of activity was recorded separately from simply moving about.

Distribution of Activity in Time

(1) *Pasture.* Figure 1 shows the result of twelve 8-hour observation periods on three individuals (See Table I). The black portions of

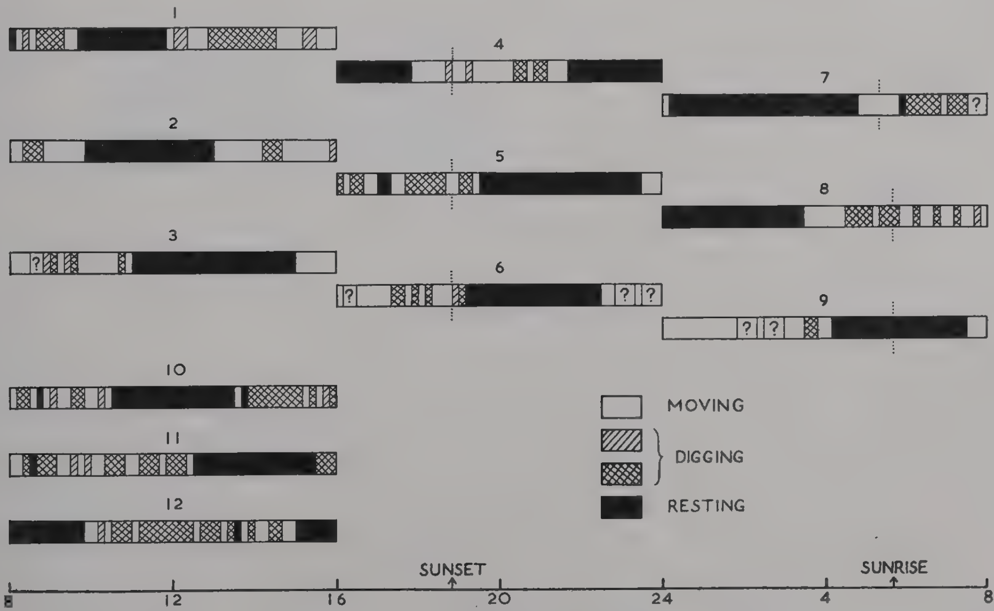

Fig. 1. Activities recorded during twelve 8-hour periods of continuous observation. (3 individuals: See Table I.)

the diagrams represent the times when the moles were resting. The records show considerable variation both in the amount of time spent in rest and in its distribution within an 8-hour period. Part of this variation is probably due to individual differences in behaviour. Part is undoubtedly due to the fact that the records were obtained on different days, for even on consecutive days the rest periods of the same individual occurred at different times (Fig. 1, 10-12). Nevertheless these records suggest that moles have three main periods of rest and three periods of activity during the 24 hours.

The average proportion of an 8-hour period spent in continuous rest was 3 hr. 30 minutes. (The average length of the 9 complete rest periods is 3 hr. 20 minutes.) The longest period of rest recorded was 4 hr. 40 minutes and the shortest 2 hr. 10 minutes. Both records were for the same animal, and in fact were obtained in the only two consecutive observation periods. The animals occasionally rested in the tunnels for periods of up to 20 minutes. Long periods of rest were always spent in the nest. It is impossible to demonstrate conclusively the existence of any 24-hour rhythm, but if the records for the six daytime periods are summed, there is evidence of a peak in resting between 1030 and 1330 hours G.M.T. (Fig. 2, 1).

In Figure 1, the blank portions of the diagrams show when the animals were moving about, the cross-hatched lines show when digging occurred more or less continuously through the entire 10-minute unit ("continuous digging"), and the single-line shading shows when only one brief outburst of digging occurred during the unit ("spasmodic digging"). During the 8-hour periods continuous digging was observed in an average of nine 10-minute units, *i.e.* digging occupied approximately one-third of the 4½ hours' activity (Table I). Spasmodic digging was observed in an average of 1.5 units.

TABLE I. *Activities recorded during 8-hour periods of continuous observation: analysis in 10-minute units*

					REST				ACTIVITY						
					In nest		*In tunnel*		*Continuous digging*†		*Spasmodic digging*		*Moving about*		
Number and sex	Date 1954	Time (G.M.T.)	Key to Fig 1	Total 10-min. units	No. units	% total	No. units	% total	No. units	% total	No. units	% total	No. units	% total	Distance moved in 8 hours (yd.)
Pasture															
A f ad...........	11.4	0800-1600	1	48	13	27.1	1	2.1	14	29.1	5	10.4	15	31.3	126
B f ad...........	16.3	" "	2	48	19	39.6	0		6 (2)	12.5	1	2.1	22	45.8	126
C m ad...........	17.3	" "	3	46*	24	52.2	0		3	6.5	2	4.3	17	37.0	137
A f ad...........	9.4	1600-2400	4	48	25	52.1	0		4	8.3	2	4.2	17	35.4	97
B f ad...........	7.4	" "	5	48	24	50.0	2	4.2	11 (3)	22.9	0		11	22.9	66
C m ad...........	8.4	" "	6	40	20	50.0	0		5	12.5	1	2.5	14	35.0	164
A f ad...........	11.4	0000-0800	7	45	28	62.3	1	2.1	8	17.8	0		8	17.8	30
B f ad...........	3.4	" "	8	48	21	43.8	0		10 (1)	20.8	1	2.1	16	33.3	128
C m ad...........	2.4	" "	9	42	20	47.6	0		2	4.8	0		20	47.6	114
B f ad...........	20.4	0800-1600	10	48	18	37.5	2	4.2	14 (1)	29.1	3	6.3	11	22.9	156
B f ad...........	21.4	" "	11	48	18	37.5	1	2.1	16	33.3	2	4.2	11	22.9	187
B f ad...........	22.4	" "	12	48	17	35.4	1	2.1	18 (7)	37.5	1	2.1	11	22.9	118
		Total		557	247	—	8	—	111 (14)	—	18	—	173	—	
		Average		—	20.6	44.34	0.67	1.44	9.3	19.93	1.5	3.23	14.3	31.06	
							45.78								
Arable															
D m juv..........	1.6	0800-1600		48	10	20.8	0		22	45.8	2	4.2	14	29.1	833
E m juv..........	2.6	" "		48	17	35.4	4	8.3	13	27.1	3	6.3	11	22.9	106
F f ad...........	3.6	0900-1700		48	15	31.3	7	14.6	14 (2)	29.1	3	6.3	9	18.7	40
E m juv..........	10.6	0800-1600		48	15	31.3	3	6.3	10	20.8	5	10.4	15	31.3	348
D m juv..........	20.6	" "		48	13	27.1	0		24 (3)	50.0	1	2.1	10	20.8	244
E m juv..........	22.6	" "		48	19	39.6	2	4.2	15 (8)	3.13	1	2.1	11	22.9	267
G m juv..........	10.7	" "		48	20	41.6	0		21 (8)	43.8	0		7	14.6	20
H m juv..........	10.7	" "		48	12	25.0	17	35.4	13 (10)	27.1	1	2.1	5	10.4	36
H m juv..........	14.7	0900-1700		48	22	45.8	9	18.7	7 (3)	14.6	2	4.2	8	16.7	116
H m juv..........	15.7	0800-1600		48	19	39.6	8	16.7	11 (11)	22.9	2	4.2	8	16.7	23
H m juv..........	23.7	" "		48	7	14.6	8	16.7	12 (4)	25.0	6	12.5	15	31.3	147
		Total		528	169	—	58	—	162 (49)	—	26	—	113	—	
		Average		—	15.4	32.01	5.3	10.99	14.1	30.68	2.4	4.92	10.3	21.40	
							43.00								

*Discrepancies due to failure to locate the animals.
†Shallow tunnels; deep tunnels with hills in brackets.

There was considerable variation between the individuals in the time occupied by digging. The male spent less time digging than either of the females. Although female B rested at different times on three consecutive days, the proportion of the active period spent in digging was the same (Fig. 1, 10-12). Continuous digging most frequently occupied one 10-minute unit only, and approximately 80% of the records did not exceed three units (Table II). The longest period of digging observed occupied ten units. It was evident from the summed records for the six daytime periods (not shown) that the digging activity was distributed evenly throughout the 8 hours.

(2) *Arable fields.* The activity rhythms of the 5 individuals in the arable fields were of the same pattern as those of the animals in pasture (Table I). The proportion of the 8-hour periods spent in rest was approximately the same (43.00% compared with 45.78%), but less time was spent in the nest (an average of only 2 hr. 30 minutes instead of 3 hr. 30 minutes) and more time was spent resting in the tunnels (Fig. 2, 2). The longest rest recorded in a tunnel was 60 minutes. As with the moles living in pasture, there are suggestions of individual differences in the rhythms: male H, for example, appears to have spent considerably more time resting than the other animals. There is no evidence, however, of a peak in resting at a particular time when the records for the eleven 8-hour periods are summed (Fig. 2, 2).

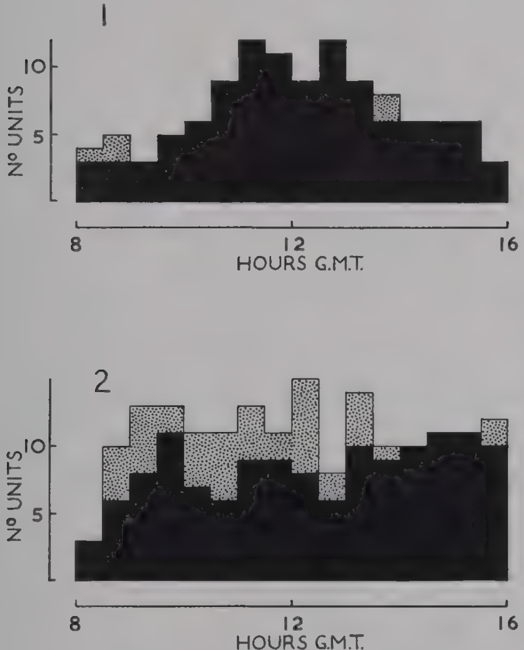

Fig. 2. Summed records for rest in (1) pasture, (2) arable fields: solid black = rest in nest; stippled = rest in tunnel; vertical scale in 10-minute units.

Table II. *Frequency of occurrence of periods of digging of different lengths*

	Duration in Ten-Minute Units										Total
	1	2	3	4	5	6	7	8	9	10	
Pasture No.....	15	9	11	2	1	1	0	2	0	1	42
%.....	*35.7*	*21.4*	*26.2*	*4.8*	*2.4*	*2.4*	..	*4.8*	..	*2.4*	*100.1*
Arable No.....	27	12	13	7	3	2	1	0	0	1	66
%.....	*40.9*	*18.2*	*19.7*	*10.6*	*4.6*	*3.0*	*1.5*	..	..	*1.5*	*100.0*

Table I shows that in arable fields the proportion of the active period spent in continuous digging averaged 2 hr. 20 minutes or nearly two-thirds of the total compared with one-third in pasture, and that the time spent moving about was correspondingly reduced. In order to test the significance of this difference the data are grouped as follows:

Number of units spent in:

	Rest		Digging		Moving about		Total
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
Pasture...	255	247.44	129	162.74	173	146.82	557
Arable....	227	234.56	188	154.26	113	139.18	528
	482		317		286		1085

The expected number of units is calculated on the assumption that there are no differences in the rhythms of the animals in the pasture and arable fields. The differences are obviously significant ($\chi^2 = 24.2$, and with 2 degrees of freedom, $P = <.001$), but unfortunately they cannot, without other evidence, be attributed to a difference in the two habitats as the observations were carried out on different classes of animals and at different seasons.

Although much more time was spent digging in the arable fields, the duration of the outbursts of continuous digging was almost exactly the same as in pasture, with one 10-minute unit the most frequent period recorded, and approximately 80% of the records lying between one and three units (Table II).

Distribution of Activity in Space

(1) *Movements.* The individuals in the pasture were consistently located within the same areas. Figure 3 shows, for example, the positions in which

female B was located during three 8-hour periods: it is clear that the area used was approximately the same in each. The tunnel-systems of the two females extended over approximately 130 sq. yd. or 1/40 acre, while that of the male extended over 280 sq. yd. or 1/17 acre. (It is likely that the male was occasionally outside its area as intensive searching failed to locate it on several occasions; see Table I.) The animals were located several times later in the year and were found within the identical areas. The male, in fact, was still using the same nest and tunnel-system in August.

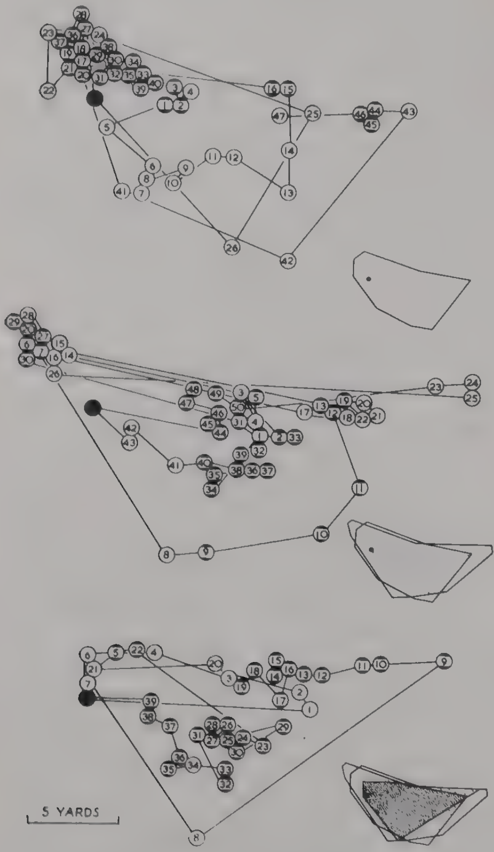

FIG. 3. Points of location of animal B on three successive days: lines join consecutive points; solid circle = nest; blocked circles show where digging was observed.

It was not possible to measure exactly the distances moved within the tunnel-systems because the animals could not be followed continuously. Sudden changes of direction often resulted in temporary loss of contact so that the exact route to the new position could not be determined. The distances between successive points of location, however, gave an approximate indication of the minimum distances moved during 8 hours (Table I). These estimates will be particularly low in those periods in which individuals occasionally could not be located. Nevertheless, they suggest that during an active period of about 4½ hours, each animal passed through at least 200 yd. of tunnel-system.

The individuals in the arable fields, on the other hand, were never located in exactly the same areas in two consecutive weeks because new tunnels were continually being built and old ones abandoned (Fig. 4). Animal H, for example, was located in area 1 on July 10, in area 2, 80 yd. away on July 14, and by July 22 it had moved to 3 (Fig. 5). It was not found again at 1 and 2. It seems probable that such extreme changes in area (and nest-site) are peculiar to juveniles, which have not yet acquired permanent homes.

The tunnel-systems in use at any one time extended over at least ¼ acre (Figs. 4 & 5) which is considerably larger than those in the pasture. The total length of tunnel in each system, however, was probably not correspondingly greater so that the difference between the two habitats is more apparent than real. A moving animal could be followed continuously with the G-M counter unit as the positions of the tunnels were revealed by raised ridges of soil: sudden changes of direction presented less difficulty than in pasture because the various alternative routes could be seen. Consequently it was possible to measure *actual* instead of *minimum* distances moved. Fig. 6 shows the relationship between the tunnel-system of animal D and the positions where it was located. This animal moved approximately 830 yd. during an active period of 6½ hours. There was greater variation than in the pasture in the total distances moved, and at the other extreme there were individuals which moved only 20-40 yd. during 8 hours (Table I).

(2) *Digging.* Each individual in the pasture normally dug in several different places during an 8-hour period, and indeed, some digging was observed throughout almost the entire area covered by the tunnel-system (Fig. 3). In the arable land, the moles also dug in several different places, but the fact that their tunnel-systems were continually being extended indicates that digging was concentrated in one particular place. Measurements of the rate of digging showed that individuals seldom constructed more than 4-6 feet of shallow tunnel during 8 hours, although a mole which was released in an unoccupied field of pasture constructed 22 yd. of shallow tunnel dur-

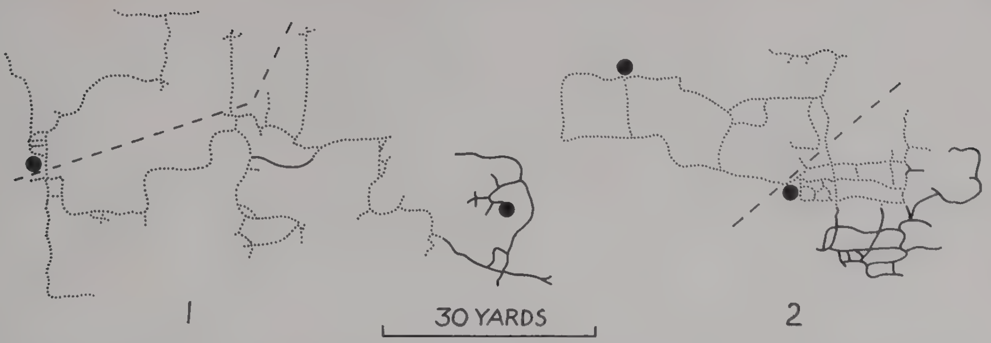

FIG. 4. (1) Animal D; (2) Animal E. New tunnels (unbroken lines) added to existing tunnel-systems during a 3-week period: broken lines show portion of original tunnel-system still in use at end of period; solid circles = nests.

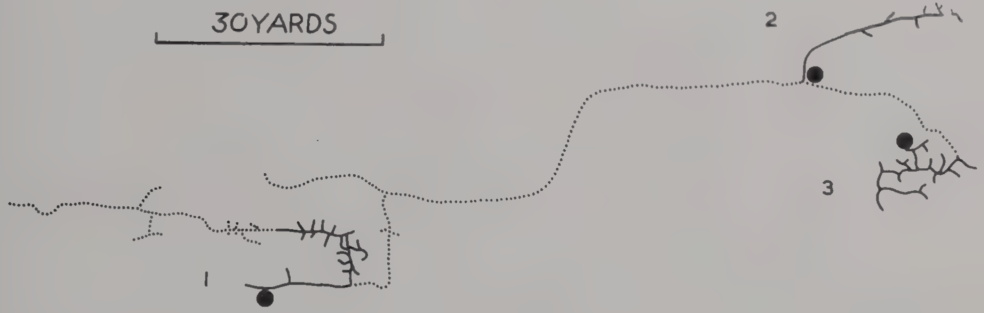

FIG. 5. New tunnels (unbroken lines) added by animal H to its tunnel-system during a 2-week period: solid circles = nests.

ing the first 24 hours. The maximum figure recorded in arable land was 12 yd. in 15 hours.

The moles in pasture were normally located in tunnels several inches below the surface. When digging, however, they were usually immediately below the surface in shallow tunnels among the roots of the grass. The digging of deep tunnels, which resulted in the formation of hills, occurred during only 14/111 ten-minute units (Table I). In the arable fields in June, shallow tunnels, covered by raised ridges of soil, were again the usual result of digging, and deeper tunnels with hills were made during only 13/88 (15%) of the units. In July, however, tunnels with hills were made during 36/64 (56%) of the units. It is generally believed that the depth at which digging occurs, and consequently the type of tunnel formed, is related to the hardness and humidity of the soil. Shallow tunnels are made when the soil is loosely packed and moist, but when it becomes hard and dry and food is no longer available at the surface, digging is confined to the deeper layers.

Some evidence was obtained on the nature of the prey captured by the moles when digging close to the surface. In the pasture, individuals were often observed seizing earthworms and fly larvae. Food was clearly abundant. During 96 hours' observation, for example, 326 worms and numerous larvae were seen emerging from the ground close to burrowing moles. Although earthworms were seen less often on the surface in arable fields, they formed a high proportion of the contents of the stomachs examined, and were evidently an important source of food. The moles were occasionally seen to leave their tunnels in pursuit of Carabid beetles.

DISCUSSION

The mole resembles *Sorex* and *Microtus* in that it is active throughout both day and night, but it differs in that it has a short-term rhythm of approximately 8 hours instead of 2½ hours. Its rhythm is, in fact, longer than that of any small mammal so far investigated. But in spite of the difference in the length of the short-term rhythms in *Talpa* and *Sorex*, the proportion of the 24 hours spent in rest is approximately the same.

When resting, the moles were usually in their nests, where they were known to sleep soundly, but some rest, especially in arable fields, was re-

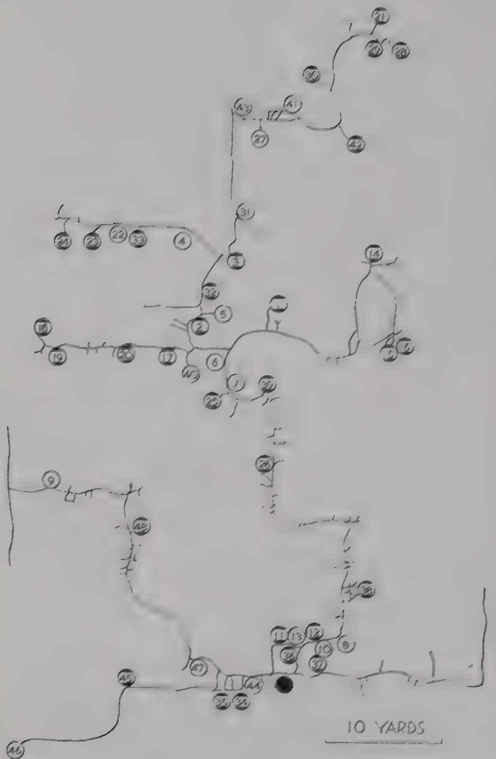

FIG. 6. Points of location of animal D during a single 8-hour period: lines show position of shallow tunnels; solid circle = nest; blocked circles show where digging was observed.

corded in the tunnels. The occurrence in *Sorex* of "short naps" outside the nest in addition to true sleep (Crowcroft 1954) suggests that the mole may also have two distinct forms of rest, true sleep, which is confined to the nest and "short naps" which occur in the tunnels. The more frequent occurrence of "short naps" in arable land may have been associated with the greater amount of digging, and consequently higher expenditure of energy, during the active periods.

It is generally believed that the short-term rhythm is controlled by hunger and that the animal is awakened by its need for food. The shorter periods of sleep in arable land may thus be an indication of a poorer food supply. An investigation, similar to that carried out by Folitarek (1932), of the stomach contents in the two habitats, might reveal whether the animals were, in fact, unable to obtain sufficient food during the course of a normal period of activity.

It is not known how much food the moles obtained without digging. It is commonly believed that certain invertebrates find their way into the deep tunnels, thus enabling the mole to obtain a proportion of its food merely by searching through its tunnel-system. Hauchecorne (1927) concluded that this was the principal method of feeding in arable fields in late summer when there were no shallow tunnels and few fresh hills were being made. Foliterak (*loc. cit.*) also believed this to be the mole's chief means of obtaining food in meadows in the Ukraine.

The fact that the moles in arable land spent two-thirds of the active period digging suggests that food was not readily available in the existing tunnels. In the pasture, however, considerably less time was spent digging, which suggests either that more food was available in the tunnels or that less digging was necessary because of a richer soil fauna. A further indication of a scarcity of food in the arable land was the fact that the tunnel-systems were continually being extended. These differences in behaviour in the two habitats were probably related to differences in the amounts of food present, but because of the different classes of animals involved, the possibility of differences in ability to obtain it cannot be excluded.

A 24-hour rhythm, with peaks in activity associated with sunrise and sunset, has been found in all species of small mammal so far investigated, although in *Sorex araneus* kept in the laboratory, this rhythm only becomes evident when the intensity as well as the duration of activity is taken into account (Crowroft *loc. cit.*). Certain workers, (Folitarek 1932, Kuzyakin 1935) have reported greater activity in *Talpa* at dusk, which they suggest is associated with an upward movement of the soil fauna at night. The information available, however, is not sufficient to demonstrate a 24-hour rhythm in the activity of the mole.

ACKNOWLEDGMENTS

I wish to thank Dr. Peter Crowcroft for criticism and for preparing the illustrations. Mr. P. H. Leslie kindly assisted with the statistical analysis. The work was carried out under Dr. L. Harrison Matthews, F.R.S. at the Zoological Society of London, and financed by the Nature Conservancy.

SUMMARY

1. Direct infomation was obtained about the activity of moles (*Talpa europaea* L.) by labelling individuals with tail-rings containing radioactive Cobalt and locating them at frequent intervals with a Geiger-Müller counter unit.

2. The individuals studied were found to have a short-term rhythm of approximately 8 hours, of

which 3½ were spent in rest. Digging occupied between one- and two-thirds of the 4½ hours' activity. The remainder of the active period was spent in moving about. There were differences in the proportion of time spent in digging and in moving about between individuals living in arable land and those in pasture.

3. The distances moved by individuals through their tunnels during an active period varied between 20 and 830 yards. The possible relationship between the amount of digging and the abundance of the prey is discussed.

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THE VEGETATIONAL STRUCTURE OF AN ABANDONED FIELD IN SOUTHEASTERN MICHIGAN AND ITS RELATION TO ENVIRONMENTAL FACTORS

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INTRODUCTION

For several years, the vegetation of an old field, representative of much abandoned land in the southeastern part of Michigan, has been under investigation as a more or less natural community. In a preliminary report (Evans and Cain 1952) attention was called to the complex, mosaic nature of the vegetation and to the confusion of distributional patterns exhibited by the various vegetational components. This patchiness has persisted from year to year and is as perplexing to explain as it is to describe. Indeed, the problems posed by this field vegetation are not unlike those which Scandinavian ecologists have faced in montane regions, where numerous stable communities may co-exist in limited areas and where the vegetational differences cannot be recognized by the presence of species which are exclusive to one or other of the several vegetational types. In these situations, the criteria that have proved most useful for classification have been (1) differences in the dominance and abundance of the species and (2) the occurrence of "differential" species, *i.e.*, those which are constant in a type and which are mainly but not exclusively confined to that type. Emphasis has also been placed upon the homogeneity of the vegetation type, by which is meant a more or less uniform probability of encountering a given assemblage of species in any sample taken from the type. The methodology of the Scandinavian school has not as yet been given extensive trial in North America. Recently, Hanson and Dahl (in press) used it to analyze some grassland communities in the mountain-front zone in northern Colorado. Their results suggested that the same techniques might be profitably applied to the relatively small-scale vegetational complexities of this old field.

A favorable opportunity to carry out such an analysis was provided by the presence of the junior author at the University of Michigan during the months of September, October, and November, 1953. This stay was made possible through a Smith-Mundt Fellowship from the United States Department of State. The vegetational and soil analyses reported in this paper were carried out jointly by both authors at the Edwin S. George Reserve of the University of Michigan. We are indebted to J. Speed Rogers, Director of the Reserve, and to Irving J. Cantrall, its Curator, for making its facilities available for this study. Dr. Cantrall also courteously provided us with climatological records taken by him at the Reserve. Rogers McVaugh very kindly determined or

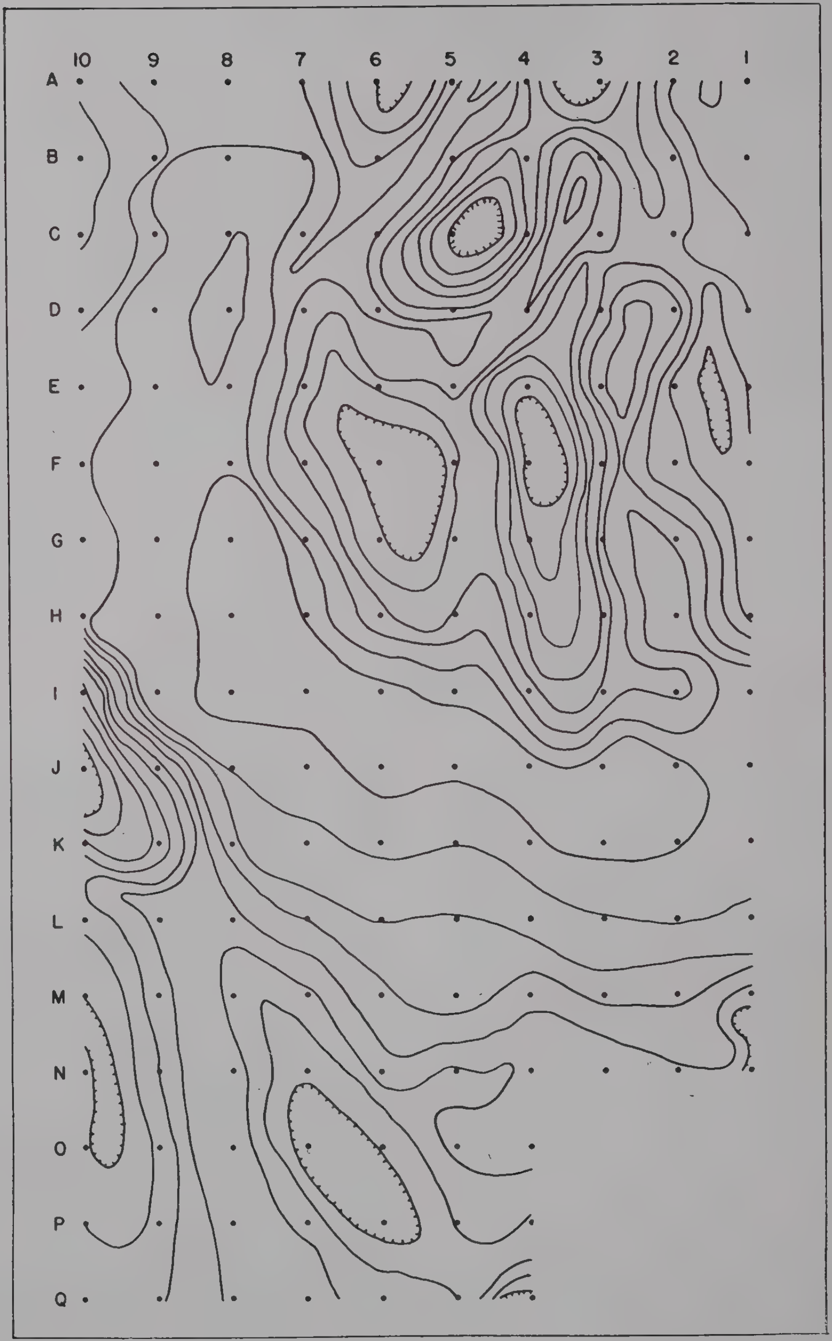

FIG. 1. Contour map of abandoned field, E. S. George Reserve, Livingston County, Michigan, constructed by F. C. Evans, D. L. Riggs, and A. M. Stebler, July, 1952. The long axis of the field is oriented directly north-south. Contour lines are 1-ft. intervals. Hatched lines indicate depressions. Dots indicate grid markers, spaced at 20-yd. intervals.

checked the identifications of most of the vascular plants. Maurice W. Senstius gave much useful advice on soil problems and graciously permitted us to use this laboratory and equipment for mechanical analyses of soil samples. Field consultation with J. O. Veatch in regard to soil types and processes was also extremely helpful. Nelson G. Hairston has allowed us to publish soil temperature and soil freezing data collected by him in his studies of the soil fauna of the field (Hairston and Byers 1954). Raymond H. Brand, Dixon L. Riggs, and Adolph M. Stebler assisted in making the contour map of the field. Evan B. Hazard and Peter J. R. Hill supplied the photographs of the various vegetation types. Pierre Dansereau kindly criticized the manuscript. This study is part of a program of community ecology under the sponsorship of the Institute of Human Biology, University of Michigan.

Description of the Field Environment

Physiography

The Edwin S. George Reserve is located approximately 4½ miles west of the village of Pinckney, in the southwestern corner of Livingston County, Michigan. It covers an area of about 2 square miles. The surrounding region has a glacial moraine and basin character, and many of its features have resulted from the action of ice and water in the ancient Huron River drainage system as it existed near the end of the Wisconsin period.

The field selected for this study is a 15-acre tract in the northeast quarter of Putnam Township, section 19. It lies on a large glacial outwash plain in the north-central portion of the Reserve, at an elevation of 1,000 feet. The field is approximately 330 x 200 m., with its long axis oriented almost due north. A series of 161 wire markers bearing identifying letters and numbers were placed at 20-yard intervals throughout the field to provide a system of localized reference points. The positions of these markers are shown in Figure 1, which is a contour map of the field. The difference between the highest and lowest levels in the field is approximately 10 feet, and the steepest slope—near J-10—does not exceed 15 per cent. The highest land extends as an irregular strip across mid-field, and the ground slopes away gently to the north and south. Glacial kettle holes of various sizes lie to the east as well as to the west, so that there is considerable drainage away from the field. Within the field, the drainage pattern is determined and clearly marked by a series of shallow, saucer-shaped depressions, varying in size from 70 to 400 m^2. These depressions are probably of glacial origin and constitute the principal physiographic feature of the field.

Climate

The Reserve is subjected to a humid, mesothermal type of climate designated as $B_1B'_1rb'_2$ in the revised classification system of Thornthwaite (1948). This climatic type is broadly characterized by a relatively low thermal efficiency, of which approximately 60 per cent is concentrated in the summer, and by precipitation at all seasons. Climatic conditions on the Reserve are well-reflected in the 40-year record of the United States Weather Bureau station at Jackson, Michigan, about 30 miles to the southwest. According to this record (U. S. Dept. Agric. 1941), the mean monthly temperature ranges from 24.7°F. in January to 73.4°F. in July, and the mean annual precipitation is 30.97 inches; the average date for the last killing frost in the spring is May 6 and for the first killing frost in the autumn is October 8, giving an average frost-free season of 155 days. Table I shows the annual march of monthly mean temperature, precipitation, and snowfall at the Reserve for the period October, 1949-September, 1954. In this five-year record, extended periods of high temperatures coupled with lack of rainfall have occurred July 21-August 8, 1950, August 22-31, 1952, and July 9-17 and August 14-September 5, 1953. Prevailing winds on the study field tend to come from the northwest.

Soils

The uplands of the Reserve, on which the field under investigation is situated, are characterized by mineral soils including a variety of sands and loams. Except in the depressions, the soil of the

Table I. *The annual march of monthly mean temperature, precipitation, and snowfall at the E. S. George Reserve, Livingston County, Michigan. Figures are averages for the period October, 1949-September, 1954. Records obtained by I. J. Cantrall*

Month	Mean temp. (°F.)	Total precip. (inches)	Total snow (inches)
October	51.9	2.59	0.05
November	39.2	2.68	9.10
December	26.4	2.73	9.68
January	25.3	2.72	8.47
February	26.2	2.74	8.40
March	31.6	3.26	7.83
April	43.7	3.75	2.19
May	56.7	2.63	0.00
June	67.8	4.10	0.00
July	70.3	2.52	0.00
August	68.1	2.18	0.00
September	61.6	2.36	0.00

field consists of a gray-brown podzolic sandy loam belonging to the Fox series. Fox sandy loam is widely distributed in this part of southeastern Michigan, and much of it is, or has been, under cultivation (Veatch, Wheeting and Bauer 1934). The surface horizon characteristically consists of a brown sandy material to a depth of 15-20 cm., below which there is a lighter colored friable sandy loam 15-35 cm. thick. This is underlain by gravelly sand mixed with clay and colored reddish-brown by the presence of iron compounds. The sand gradually gives way to a gray gravel at a depth of several feet. The organic content of the cultivated soil is slight, and there is little or no lime at the surface, although the gravel substratum effervesces readily with the addition of HCl. The soil is porous and in areas of good drainage, such as this field, is not very retentive of moisture. Consequently, the frequent lack of precipitation in the middle or later part of the growing season is probably an important limiting fatcor in crop production on Fox sandy loam.

In the depressions of the field, the surface material contains relatively high proportions of silts and clays and classifies texturally as silt loam. This has accumulated to a depth of at least 1 m. in some of the depressions. Beneath it, the soil profile is developed in much the same manner as that of the field uplands. Because of its topographic position, its texture, and its dense covering of vegetation, the silt loam retains considerably more moisture than the sandy loam on the higher parts of the field. The silt loam also has a higher organic content than the sandy loam.

Cultural history

The eastern and western margins of the field are flanked by fairly extensive tracts of second-growth oak-hickory woods. It is evident that this same forest type at one time covered the land now occupied by the field vegetation. Soil samples taken at several sites on the field have yielded small pieces of charcoal at depths of 20 or 25 cm., suggesting recourse to fire in the process of clearing. The old fence lines are still in evidence but are slowly being obscured by the regeneration of forest trees, especially black oaks. There are also traces of what appear to have been furrows. No historical records are available to provide an accurate dating of cultural events relating to this particular field, but Cantrall (1943) has outlined briefly the history of the farms which were incorporated into the Reserve. Most of the clearing of these farms lands is thought to have been done by 1870. Cultivation of the upland fields was general until about 1900, but soon thereafter they were increasingly abandoned to pastures. The field under study was serving as a pasture in 1927-28, when the lands were purchased and fenced as a game preserve by Colonel George. Since this date there has been no extensive grazing on the field by domestic stock, except for an occasional horse, nor have there been any fires. The only known major disturbance to which the vegetation has been subject in the past twenty-five years has come from a herd of white-tailed deer (*Odocoileus virginianus*). These animals are the descendants of an initial stock of four does and two bucks established by Colonel George in 1928, which in the next five years increased to 160 head (Hickie 1937) but which have since been held down by annual cropping to a herd of 50 or 60 animals. Although these deer wander at large over the 1,200 acres of the Reserve, the pressure of their foraging on the field is clearly seen in the stunted growth of the numerous young junipers and hawthorns, as well as in the many topped specimens of *Solidago, Liatris, Hieracium,* and other forbs. It appears that the browsing of the deer and the general sterility of the soil are important factors impeding the progress of a return to forest conditions.

MATERIALS AND METHODS

"The ultimate parts of the community are the individual plants," as Watt (1947) has pointed out, "but a description of it in terms of the characters of these units and their spatial relations to each other is impracticable at the individual level. It is, however, feasible in terms of the aggregates of individuals and of species which form different kinds of patches; these patches form a mosaic and together constitute the community." Recognition of the patch as a basis for classification of vegetational components formed the point of departure for the present study. Superficially this old-field community presented a fairly uniform appearance, but closer inspection showed that the vegetation was in fact composed of a number of distinct elements of diverse size and nature. The most obvious patches consisted of dense stands of *Poa pratensis* L.; these ranged in size from 70 to 400 m^2. and occupied the field depressions. In these places, *P. pratensis* retains its greenness throughout much of the year, in contrast to the more distinctly seasonal vegetation of the field "uplands." Snow accumulation causes heavy matting of the *P. pratensis* patches but has little effect on the dried-out culms and stems of the "upland" plants. In addition, *P. pratensis* comes into flower at an earlier date than any of the other dominant grasses of the field. Consequently, there is almost always a marked phenological contrast between the depressions and the more elevated areas. These higher parts are dominated by *Poa compressa* L. and *Aristida purpurascens* Poir., which are sometimes found separately as "pure" stands but which occur more frequently together in patches up to 500 m^2. in extent. Scattered within and between these *Poa-Aristida* patches were numerous aggregates of lesser size and significance, including, for example, colonies of *Rubus flagellaris* Willd., *Lespedeza capitata* Michx., and *Solidago juncea* Ait., and clones of *Antennaria neglecta* Greene and *Polytrichum juniperinum* Hedw. It was evident that these various patches represented several orders of vegetational importance. The clones and colonies generally owed their distinctness to the dense cover of a single species. In some cases, such as the *Lespedeza* and *Solidago* colonies, density of cover seemed subordinate to conspicuousness of life form (thick stems, bright flowers, etc.) as a determinant of local physiognomy. Still other patches were produced, not by the dominance of some one species, but rather by the characteristic association of several, as for example in the combination of *Poa compressa, Aristida purpurascens, Solidago nemoralis* Ait., and *Rumex acetosella* L. The various types of patches contributed in different measure to the mosaic pattern of vegetation, but their relationships to each other and to the physical environment were by no means apparent. They frequently graded into one another without perceptible zones of transition and presented a picture of seemingly haphazard distribution.

The amount and variety of patchiness, the irregularity of distribution, and the degree of intergradation made it impractical to map the vegetation or to attempt analysis by means of random sampling. After considerable preliminary study, a number of types of vegetation were recognized on the basis of visible physiognomic differences. In each vegetation type, 5 to 10 plots were selected for phytosociological study. These sample plots were deliberately chosen as representative of relatively homogeneous and distinctive stands. The irregular shape of most stands made it undesirable to adopt a standard plot size, and the area of the plots ranged from 4 m^2. to 15 m^2., with no plot dimension less than 2 m. When the general location of a plot was agreed upon, its corners were marked by stakes and its center was recorded in terms of the distance and bearing from the nearest grid marker shown in Figure 1. With one or two exceptions, each plot was placed in a separate stand. A record was also made of the plot dimensions and of the direction and degree of slope.

Following the selection of a sample plot, an attempt was made to assess the total cover for each stratum of the vegetation. Two strata were recognized, one which included all forbs and grasses and is here called the C stratum, and one which included the mosses and lichens and is called the D stratum. Total cover for a given stratum was estimated in terms of the per cent of the total plot area occupied by a vertical projection onto the ground surface of all living parts of the members of that stratum. The per cent of the total area occupied by bare soil was also estimated. Next, a complete list of the species of vascular plants, mosses, and lichens found in the plot was compiled. Then the cover contributed by each species was assessed according to a scale devised by Domin (1923) and modified by the junior author. As used in the present investigation, the scale was as follows:

+ = occurring as a single individual with reduced vigor; no measurable cover.
1 = occurring as one or two individuals with normal vigor; no measurable cover.
2 = occurring as several individuals; no measurable cover.
3 = occurring as numerous individuals but with cover less than 4 per cent of the total area.
4 = cover about 1/20 (4 to 10 per cent) of the total area.
5 = cover about 1/5 (11 to 25 per cent) of the total area.
6 = cover 1/4 to 1/3 (26 to 33 per cent) of the total area.
7 = cover 1/3 to 1/2 (34 to 50 per cent) of the total area.
8 = cover 1/2 to 3/4 (51 to 75 per cent) of the total area.
9 = cover 3/4 to 9/10 (76 to 90 per cent) of the total area.
10 = cover 9/10 to complete (91 to 100 per cent).

It should be noted that the grades +, 1, 2, and 3 are concerned with abundance and vigor while those from 4 to 10 are true cover estimates. The former are useful in indicating differences when cover is apparently negligible. The various grades are of course assessments and not measurements, but in the hands of an experienced person they are a reasonably dependable means of indicating the order of magnitude of cover. When greater accuracy is not required, use of such a scale saves an appreciable amount of time. In this study, 10 plots were usually completed in one day, as compared to a maximum of 2 or 3 which could have been charted or studied by more precise quantitative methods. Not more than 2 plots of any given vegetation type were examined in any one day.

When the vegetation analysis on a given plot was completed, a soil pit was dug and the general characteristics of the soil profile were noted, especially the thickness of the humified, uppermost layer of the soil and the depth below the ground surface of the light-colored sandy loam. A number of the sample plots were subsequently revisited, and specimens of several hundred grams of soil were removed at a depth of 2-7 cm. in pits adjacent to the original ones. These specimens and a number of additional samples from the woodlots adjoining the field were brought into the laboratory and subjected to mechanical analysis by the Bouyoucos (1935) hydrometer method. Readings of pH were also taken in the laboratory, using a glass electrode for some measurements and for others a Soiltex kit prepared by the Soil Science Department, Michigan State University.

Phytosociological Analysis, Classification, and Description of Vegetation Types

Sixty-five plots were examined by the procedure which has just been outlined. This examination led to the recognition of 11 types of vegetation which were judged to be sufficiently distinct to warrant description. The phytosociological data for these types have been summarized in Tables II, III and IV. These tables indicate the total cover of vegetation in the C and D strata, the number of species encountered in each stratum, and the frequency of occurrence and range of cover estimates for each species in the plots of each type.

It was evident that the types were not all of equal rank. Some of them appeared to represent different phases of the same vegetational entity, differing principally by the replacement of one dominant species with another. An attempt was made to group the types according to the similarity of their phytosociological characteristics. Nine of the 11 types were arranged in 4 Groups, one of

TABLE II. *Values for selected vegetational and soil characteristics of the vegetation types of an old-field community, E. S. George Reserve, Livingston County, Michigan. Types are numbered as follows: (1)* Poa pratensis, *(2)* Setaria glauca, *(3)* Poa compressa, *(4)* Poa-Aristida, *(5)* Aristida-Lespedeza, *(6) Bryoid*-Antennaria, *(7) Bryoid*-Antennaria-Lespedeza, *(8) Bryoid*-Antennaria-Liatris, *(9) Bryoid*-Panicum depauperatum, *(10)* Leptoloma cognatum, *(11)* Solidago rigida

Type number	1	2	3	4	5	6	7	8	9	10	11
Number of plots examined	6	5	7	10	5	5	7	5	5	5	5
Size of plots (m^2)											
Range	6–9	2–6	5–12	4–10	6–9	6–9	4–9	7–12	5–7	5–9	6–15
Average	7.5	4.0	8.2	6.3	7.0	6.8	5.9	8.8	5.9	8.2	8.2
Total cover of C stratum (%)											
Range of plot values	100	90–100	40–60	50–80	40–60	30–50	30–50	30–40	15–40	80–100	40–70
Average	100	97	44	66	48	38	37	32	27	88	52
Total cover of D stratum (%)											
Range of plot values	0	0	0–10	10–60	30–70	30–70	30–80	30–70	50–80	0–50	0–30
Average	0	0	2	36	54	54	60	60	68	15	16
% of area in bare soil											
Range of plot values	0	0	0	0–10	0–10	15–40	10–30	10–20	10–30	0–10	0–10
Average	0	0	0	5	5	25	15	15	15	5	5
No. of species in C stratum											
Range of plot values	3–7	6–11	8–19	12–22	13–17	11–16	11–18	11–15	12–16	7–14	15–22
Average	5.3	8.4	11.6	14.9	15.2	13.6	13.7	13.0	13.0	13.4	17.2
No. of species in D stratum											
Range of plot values	0	0–3	0–7	4–6	4–7	6–8	5–7	4–7	6–11	2–6	3–8
Average	0	0.8	2.4	4.4	5.2	7.0	6.1	6.0	8.2	3.6	5.0
Depth to plow line (cm.)											
Range of plot values	—	18–22	20–28	18–40	19–23	15–25	16–20	19–23	15–20	22–25	18–30
Average	—	20.0	24.3	26.1	21.1	18.8	18.0	20.6	18.0	23.0	25.0
Humification depth (cm.)											
Range of plot values	—	—	1–5	2–3	1–3	1–3	1–3	1–3	1–3	1–5	1–4
Average	—	—	3.0	2.3	1.8	1.3	1.3	2.4	1.3	3.0	3.0

TABLE III. *Frequency of occurrence of plant species in plots of the vegetation types of an old-field community, E. S. George Reserve, Livingston County, Michigan. Types are numbered as follows: (1)* Poa pratensis, *(2)* Setaria glauca, *(3)* Poa compressa, *(4)* Poa-Aristida, *(5)* Aristida-Lespedeza, *(6) Bryoid*-Antennaria, *(7) Bryoid*-Antennaria-Lespedeza, *(8) Bryoid*-Antennaria-Liatris, *(9) Bryoid*-Panicum depauperatum, *(10)* Leptoloma cognatum, *(11)* Solidago rigida

TABLE III—*Continued*

Type number	1	2	3	4	5	6	7	8	9	10	11
Number of plots examined	6	5	7	10	5	5	7	5	5	5	5
	Number of plots of occurrence										
The C stratum											
Grasses and sedges											
Aristida purpurascens Poir.	1	3	7	10	5	5	7	5	5	3	4
Carex muhlenbergii Schkuhr	0	0	0	0	0	1	0	1	0	0	0
C. pensylvanica Lam.	0	0	0	0	0	2	0	0	2	0	0
Cyperus filiculmis Vahl	0	0	0	3	3	2	5	0	3	0	1
Danthonia spicata (L.) Beauv.	0	0	0	2	0	0	0	0	1	0	0
Leptoloma cognatum (Schultes) Chase	0	0	4	0	1	1	1	0	0	5	2
Panicum depauperatum Muhl.	0	0	0	6	0	1	2	2	5	0	2
P. lanuginosum Ell.	0	0	0	0	0	1	0	1	0	0	0
P. oligosanthes Schultes	2	3	2	3	3	1	3	2	2	1	0
P. sphaerocarpon Ell.	0	0	0	0	0	1	0	0	0	0	1
Phleum pratense L.	0	0	1	0	1	0	0	0	0	0	0
Poa compressa L.	0	0	7	10	5	4	7	4	5	5	5
P. pratensis L.	6	5	2	0	0	0	0	0	0	5	3
Setaria glauca (L.) Beauv.	5	5	0	0	0	0	0	0	0	1	2
Forbs											
Achillea millefolium L.	0	0	0	2	0	0	0	0	0	0	1
Ambrosia artemisiifolia L.	0	1	6	5	4	0	0	0	0	3	4
Anemone cylindrica Gray	0	0	0	0	2	0	0	0	0	1	2
Antennaria fallax Greene	0	0	1	5	1	4	6	5	3	0	2
A. neglecta Greene	0	0	0	8	3	5	7	5	5	0	4
Asclepias syriaca L.	6	2	0	0	1	0	0	0	0	1	0
Desmodium illinoense Gray	0	0	0	0	0	0	0	0	0	0	2
Erigeron canadensis L.	0	1	0	0	0	0	0	0	0	1	0
E. strigosus Muhl.	0	0	3	3	2	0	0	0	0	1	0
Euphorbia corollata L.	0	0	0	1	0	0	2	0	1	0	1
Gnaphalium obtusifolium L.	0	0	5	9	5	0	1	3	0	3	3
Hedeoma hispida Pursh	0	1	1	1	0	0	2	0	1	1	2
Hieracium gronovii L.	0	1	1	9	3	2	5	4	2	3	2
H. longipilum L.	0	0	3	10	3	5	7	5	3	3	3
Houstonia longifolia Gaertn.	0	0	0	1	0	0	0	0	0	0	1
Hypericum perforatum L.	0	0	0	0	5	0	1	0	0	0	0
Lactuca spp.	0	0	0	3	1	0	0	0	0	3	2
Lechea villosa Ell.	0	0	0	0	0	0	0	0	2	0	1
Lespedeza capitata Michx.	0	0	3	6	5	4	7	2	1	1	3
Liatris aspera Michx.	0	0	0	2	2	3	4	5	3	0	1
Oxalis stricta L.	1	3	1	4	1	0	0	1	0	4	3
Physalis heterophylla Nees	2	0	3	1	0	0	1	0	0	0	0
Polygonum convolvulus L.	2	1	0	0	0	0	0	0	0	0	0
P. tenue Michx.	0	0	0	3	3	3	7	1	2	0	2
Potentilla argentea L.	0	0	1	0	0	0	0	0	0	0	1
P. intermedia L.	0	0	1	1	0	0	0	0	0	0	0
P. simplex Michx.	0	1	0	1	0	0	0	0	0	0	0
Rumex acetosella L.	5	5	5	10	5	5	7	5	5	5	5
Solidago juncea Ait.	0	0	1	0	1	2	3	1	1	0	4
S. nemoralis Ait.	0	2	4	10	5	5	7	5	5	3	5
S. rigida L.	0	0	1	3	2	3	2	5	2	3	5
Tragopogon pratensis L.	0	2	5	5	2	0	0	0	0	3	0
Viola sagittata Ait.	0	1	0	0	0	0	0	0	0	0	0
The D stratum											
Mosses											
Brachythecium sp.	0	0	1	1	0	0	0	0	0	0	0
Ceratodon purpureus (Hedw.) Brid.	0	0	2	8	5	5	7	5	5	3	2
Polytrichum juniperinum Hedw.	0	0	0	0	0	1	1	2	0	1	2
P. piliferum Hedw.	0	0	0	4	2	5	6	4	4	1	3
Lichens											
Cladonia clavulifera Tuck.	0	0	0	0	1	5	6	1	5	0	0
C. cristatella Tuck.	0	1	5	10	5	5	7	5	5	5	5
C. nemoxyna (Ach.) Coem.	0	1	1	10	5	5	7	5	3	4	4
C. pyxidata (L.) Fr.	0	1	2	10	5	5	7	5	5	0	0
C. verticillata Hoffm.	0	0	0	1	1	4	2	2	5	0	2
Lecidea granulosa (Ehrh.) Ach.	0	0	0	1	0	0	0	0	2	0	0
Peltigera spuria (Ach.) DC.	0	0	0	3	0	0	0	1	1	0	1
Total species recorded	9	19	28	38	33	29	30	28	30	27	38

which included the "upland" types. Two types could not be readily classified and their status is therefore uncertain. A major cleavage was recognized to exist between the Group of "depression" types and the Groups which included the "upland" types. These two principal subdivisions of the old-field vegetation appear to represent "associations" of the same order of magnitude as many of those which are being described by European ecologists.

The following descriptions are based on this analysis and classification. Species with high cover values, visual prominence, and occurrence in nearly all the plots examined for the Group are here termed dominants. Species which occurred in 80 per cent or more of the plots belonging to one Group but which generally had low cover values are called constants. Differential species are the dominants and constants which were mainly but not exclusively confined to a given Group; they have been marked by asterisks. Other symbols used are as follows: TC, total cover in the C or herbaceous stratum; TD, total cover in the D or ground stratum; TS, total bare soil; NC, number of species in the C stratum; ND, number of species in the D stratum.

Subdivision A. Vegetation of the depressions

This vegetation owes its very distinctive character to the overwhelming predominance of *Poa pratensis,* which produces a thick sod and a dense and luxuriant growth of leaves. Few other grasses or forbs are able to establish themselves successfully, although *Asclepias syriaca* L., with its deep rhizome system, often forms conspicuous clones. The depression vegetation frequently assumes a distinctly zonal character, with *P. pratensis* occupying the central areas and with a marginal belt of *Setaria glauca* (L.) Beauv., generally from 3 to 6 feet in width, which is especially prominent in August and September when it has developed fruiting heads. Two vegetation types were recognized in the depressions; these were classified as belonging to the same Group.

TABLE IV. *Ranges of cover estimates of plant species in plots of the vegetation types of an old-field community, E. S. George Reserve, Livingston County, Michigan. Types are numbered as follows: (1)* Poa pratensis, *(2)* Setaria glauca, *(3)* Poa compressa, *(4)* Poa-Aristida, *(5)* Aristida Lespedeza, *(6) Bryoid*-Antennaria, *(7) Bryoid*-Antennaria-Lespedeza, *(8) Bryoid*-Antennaria-Liatris, *(9) Bryoid*-Panicum depauperatum, *(10)* Leptoloma cognatum, *(11)* Solidago rigida. *The cover estimate scale is that of Domin (1923), slightly modified (cf. text)*

Type number	1	2	3	4	5	6	7	8	9	10	11
Number of plots examined	6	5	7	10	5	5	7	5	5	5	5
The C stratum Grasses and sedges	Cover estimates in plots of occurrence										
Aristida purpurascens Poir.	1	1–2	1–3	6–8	5–6	3–4	2–4	2–4	1–3	1	2–3
Carex muhlenbergii Schkuhr	0	0	0	0	0	1	0	1	0	0	0
C. pensylvanica Lam.	0	0	0	0	0	1	0	0	3–4	0	0
Cyperus filiculmis Vahl	0	0	0	1–2	2–3	1–2	1–3	0	2–3	0	2
Danthonia spicata (L.) Beauv.	0	0	0	1–2	0	0	0	0	1	0	0
Leptoloma cognatum (Schultes) Chase	0	0	1–3	0	3	2	3	0	0	6–8	1
Panicum depauperatum Muhl.	0	0	0	1–3	0	1–3	1	2–3	4–6	0	2
P. lanuginosum Ell.	0	0	0	0	0	2	1	0	0	0	0
P. oligosanthes Schultes	+–1	+–1	1–2	1–3	2–3	1	1	+–1	+–2	1	0
P. sphaerocarpon Ell.	0	0	0	0	0	3	0	0	0	0	1
Phleum pratense L.	0	0	1	0	2	0	0	0	0	0	0
Poa compressa L.	0	0	7–8	3–7	3–5	2–3	1–4	3–5	2–3	3–6	3–4
P. pratensis L.	10	8–9	1–3	0	0	0	0	0	0	3–8	1–5
Setaria glauca (L.) Beauv.	1–2	6–7	0	0	0	0	0	0	0	1	1
Forbs											
Achillea millefolium L.	0	0	0	1–3	0	0	0	0	0	0	0
Ambrosia artemisiifolia L.	0	1	1–4	1	1	2–3	1	1	1	1–3	2
Anemone cylindrica Gray	0	0	0	0	1–2	0	0	0	0	+–1	1
Antennaria fallax Greene	0	0	2	1–5	2	1–6	1–5	1–3	1–2	0	1
A. neglecta Greene	0	0	0	1–3	1–3	2–7	1–6	2–6	1–5	0	2
Asclepias syriaca L.	2–4	1	0	0	1	0	0	0	0	+	0
Desmodium illinoense Gray	0	0	0	0	0	0	0	0	0	0	1–2
Erigeron canadensis L.	0	3	0	0	0	0	0	0	0	+	0
E. strigosus Muhl.	0	0	2–4	1–2	1–3	0	0	0	0	1	0
Euphorbia corollata L.	0	0	0	1	0	0	2	0	1	0	1
Gnaphalium obtusifolium L.	0	0	1–2	1–3	1–2	0	1	1	0	1–2	1
Hedeoma hispida Pursh	0	1	1	1	0	0	1	0	1	1	1
Hieracium gronovii L.	0	1	1	1–2	2	2	+–1	1–3	1	1–2	1
H. longipilum L.	0	0	1	2–3	2–3	1–3	1–3	2–4	2–3	1–2	1–2
Houstonia longifolia Gaertn.	0	0	0	1	0	0	0	0	0	0	0
Hypericum perforatum L.	0	0	0	0	+	0	2	0	0	0	0
Lactuca spp.	0	0	0	2	1	0	0	0	0	1–2	2–3
Lechea villosa Ell.	0	0	0	0	0	0	0	0	2–3	0	1
Lespedeza capitata Michx.	0	0	+–1	1–2	3–4	+–2	3–4	+–1	2	1	1–2
Liatris aspera Michx.	0	0	0	+–2	3	3	1–4	4–5	+–4	0	1
Oxalis stricta L.	1	1–3	1	1–2	1	0	0	+	0	1–3	1–3
Physalis heterophylla Nees	1–2	0	1–2	1	0	0	1	0	0	0	0
Polygonum convolvulus L.	1	1	0	0	0	0	0	0	0	0	0
P. tenue Michx.	0	0	0	1–2	1	1–2	1–3	1	1–2	0	1–2
Potentilla argentea L.	0	0	1	0	0	0	0	0	0	0	+
P. intermedia L.	0	0	1	1	0	0	0	0	0	0	0
P. simplex Michx.	0	3	0	3	0	0	0	0	0	0	0
Rumex acetosella L.	1–5	3–5	1–4	2–3	3–4	1–3	2–3	2–3	2–3	2–4	2–3
Solidago juncea Ait.	0	0	3	0	2	2–3	1–2	4	1	0	1–3
S. nemoralis Ait.	0	1–2	1–2	3–6	1–5	3–5	2–5	2–4	3–4	1–2	1–3
S. rigida L.	0	0	2	1–2	1–2	1–3	1–2	1–3	1–2	2	5–7
Tragopogon pratensis L.	0	1	1–2	1–2	2	0	0	0	0	1–3	0
Viola sagittata Ait.	0	3	0	0	0	0	0	0	0	0	0
The D stratum Mosses											
Brachythecium sp.	0	0	1	1	0	0	0	0	0	0	0
Ceratodon purpureus (Hedw.) Brid.	0	0	1–4	1–5	3–6	3–7	5–8	2–6	6–8	+–2	1–3
Polytrichum juniperinum Hedw.	0	0	0	0	0	2	4	3–4	0	3	1
P. piliferum Hedw.	0	0	0	1–5	3	2–8	2–7	3–7	2–6	1	1–2
Lichens											
Cladonia clavulifera Tuck.	0	0	0	0	5	2–3	1–4	3	3–5	0	0
C. cristatella Tuck.	0	2	+–3	3–7	5–7	3–5	3–8	4–5	3–7	1–6	+–3
C. nemoxyna (Ach.) Coem.	0	+	3	1–5	3–4	1–3	1–4	1–3	2–3	1–5	2–3
C. pyxidata (L.) Fr.	0	1	2–3	1–5	2–5	1–4	1–3	3	1–5	2–4	3–5
C. verticillata Hoffm.	0	0	0	1	2	2–3	2–3	1–3	1–4	0	1–3
Lecidea granulosa (Ehrh.) Ach.	0	0	0	1	0	0	0	0	1–3	0	0
Peltigera spuria (Ach.) DC.	0	0	0	1–2	0	0	0	1	1	0	1

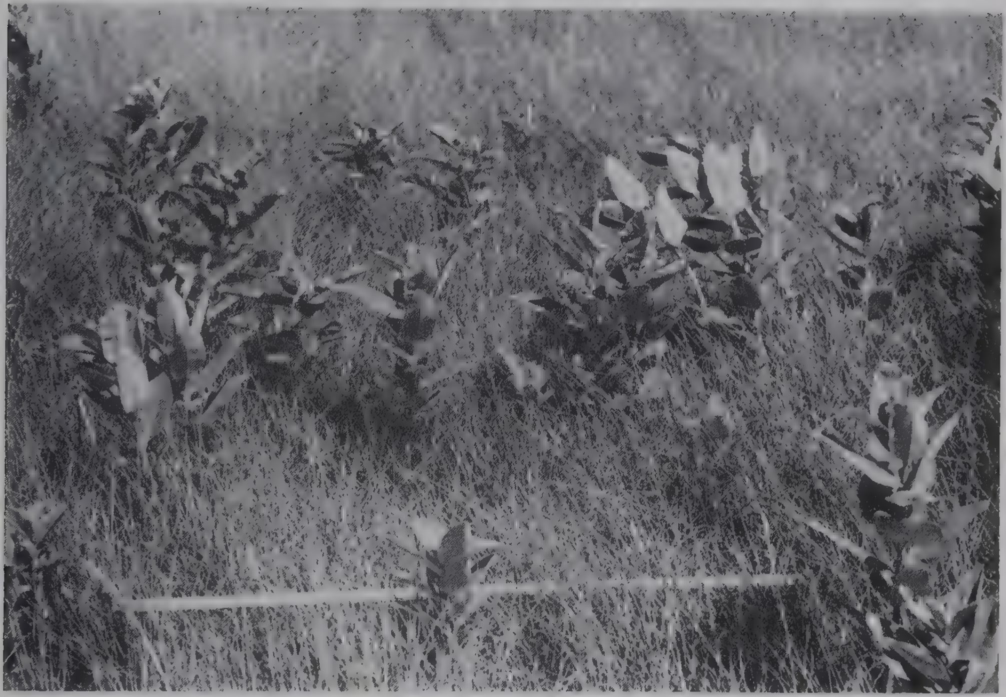

FIG. 2. *Poa pratensis* vegetation type, June 12, 1954. The dense grass eliminates most forbs, but *Asclepias syriaca* is an exception. Photograph by E. B. Hazard.

Group 1. *Poa pratensis* types (Figure 2). These types are characterized, not only by the dominance of *P. pratensis,* but also by the absence of the D stratum or any exposed soil. Mosses and lichens are rare and, as noted above, the number of higher plant species is small. Several species, however, such as *Viola sagittata* Ait. and *Polygonum convolvulus* L., were found only in these types.

General characteristics: TC, high (90-100 per cent). TD, zero. TS, zero. NC, low (3-11). ND, very low (0-3). Total species, 20.

Dominants: *Poa pratensis**.

Constants: *Setaria glauca**, *Asclepias syriaca, Rumex acetosella.*

Observed tpyes: The *Poa pratensis* type proper (Type No. 1), occupying the depression centers, is characterized by a very low NC (3-7) and by the complete dominance of *P. pratensis.* The *Setaria glauca* type (Type No. 2), which is always peripheral to the *Poa pratensis* type, has a somewhat higher NC (6-11) and has *S. glauca* as a codominant with *P. pratensis.*

Subdivision B. Vegetation of the uplands

The upland vegetation is much more variable than that of the depressions. It is more open in character and a dense sod is never formed. *Poa pratensis* occurs only as scattered and somewhat depauperate individuals. *Poa compressa* and *Aristida purpurascens* are the principal dominants, but a number of other grasses, especially *Panicum* spp., are of frequent occurrence. There are about 75 species of forbs, the most conspicuous of which are *Solidago nemoralis, Rumex acetosella, Hieracium longipilum* Torr., *H. gronovii* L., *Antennaria neglecta, A. fallax* Greene, *Lespedeza capitata, Liatris aspera* Michx., and *Erigeron strigosus* Muhl. There is great variation in the amount of bare soil and in the extent of the ground vegetational stratum, although the latter is often well-developed and prominent. Seven types of upland vegetation were recognized and classified in 3 distinct Groups.

Group 2. *Poa compressa* types (Figure 3). Characterized by the predominance of *P. compressa,* which produces a uniformly homogeneous stand. The dead culms of this species tend to bend over without breaking free of the rootstock and form a fairly dense matting a short distance above the soil surface, apparently preventing the successful establishment of a ground stratum. Few other higher plants are found except as scattered individuals. *Antennaria* seedlings are numerous but rarely mature.

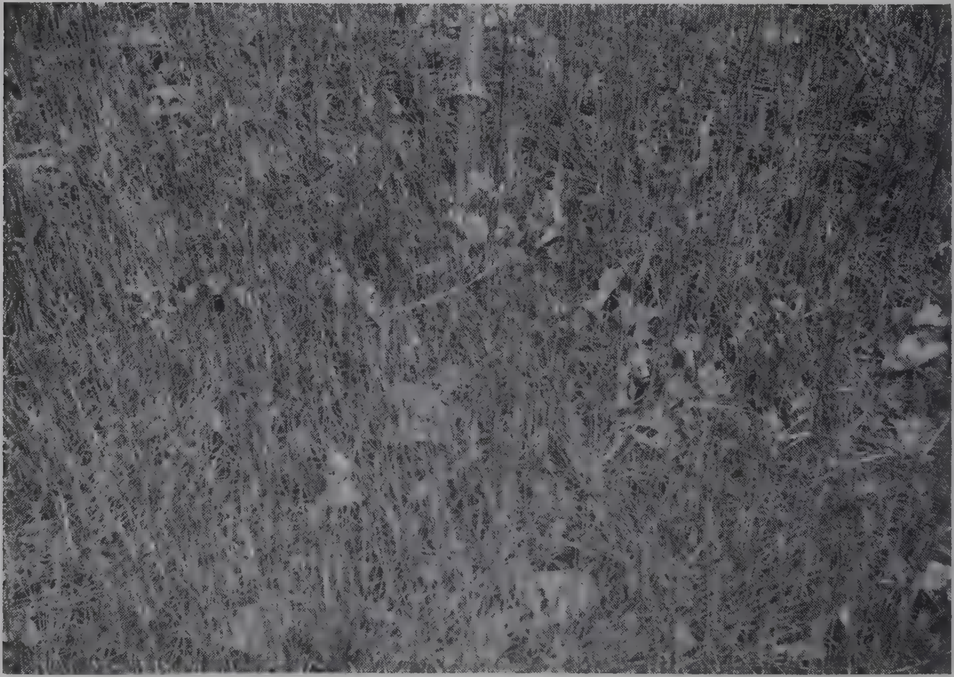

FIG. 3. *Poa compressa* vegetation type, July 8, 1954. Note the very great uniformity, the accumulation of leaf litter and the absence of a ground stratum. Photograph by P. J. R. Hill.

General characteristics: TC, medium and with little variation (40-60 per cent). TD, very low (0-10 per cent). TS, zero. NC, variable (9-19). ND, very low (0-3). Total species, 28.

Dominants: *Poa compressa.*

Constants: *Aristida purpurascens, Ambrosia artemisiifolia* L.*

Observed types: Only one type (Type No. 3) was recognized, but its general character is so distinct from all other upland types as to warrant assignment to a separate Group.

Group 3. *Poa-Aristida* types (Figures 4 and 5). These types comprise the bulk of the upland vegetation. They are characterized by the co-dominance of *P. compressa* and *A. purpurascens* and by the large number of other species in the C stratum. The *Cladonia*-dominated ground stratum is usually so well-developed that there is very little bare soil.

General characteristics: TC, medium to high (40-80 per cent). TD, variable but usually high (10-70 per cent). TS, low (0-10 per cent). NC, variable but usually high (12-22). ND, medium (4-7). Total species, 45.

Dominants: *Poa compressa, Aristida purpurascens, Cladonia cristatella* Tuck.

Constants: *Antennaria neglecta, Gnaphalium obtusifolium* L.*, *Hieracium gronovii**, *H. longipilum, Rumex acetosella, Solidago nemoralis, Ceratodon purpureus* (Hedw.) Brid., *Cladonia pyxidata* (L.) Fr., *C. nemoxyna* (Ach.) Coem.

Observed types: Two types were recognized. The *Poa-Aristida* type proper (Type No. 4) has a higher total cover in the C stratum and a lower total cover in the D stratum. The *Aristida-Lespedeza* type (Type No. 5) is distinguished by the prominence of *L. capitata* in the C stratum and of the moss *Ceratodon purpureus* in the D stratum.

Group 4. Bryoid-*Antennaria* types (Figures 6, 7, 8 and 9). These types are marked by the sparse growth of grasses and forbs and by the resulting conspicuousness of the ground stratum of mosses and lichens (which are conveniently referred to collectively as "bryoids"). *Poa* and *Aristida* have lost their dominance, and the number of species of forbs is smaller than that of the preceding Group.

General characteristics: TC, variable but usually low (15-40 per cent). TD, generally high (30-80 per cent). TS, comparatively high (10-40 per cent). NC, variable but usually medium

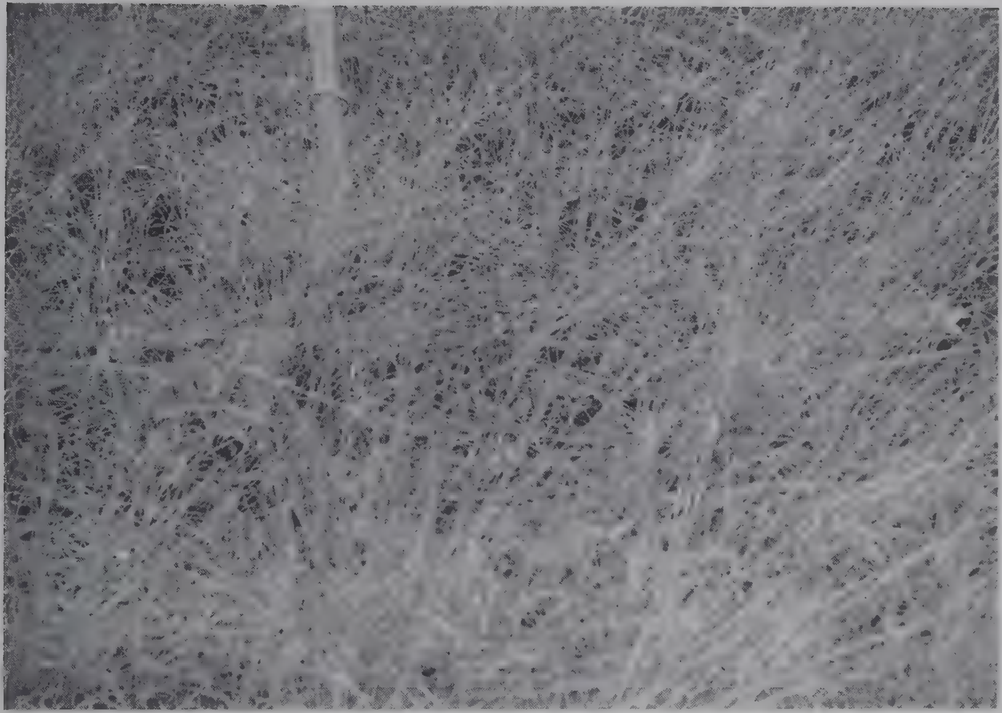

FIG. 4. *Poa-Aristida* vegetation type, July 8, 1954. The two grasses dominate but do not exclude other species and permit some development of the ground stratum. Photograph by P. J. R. Hill.

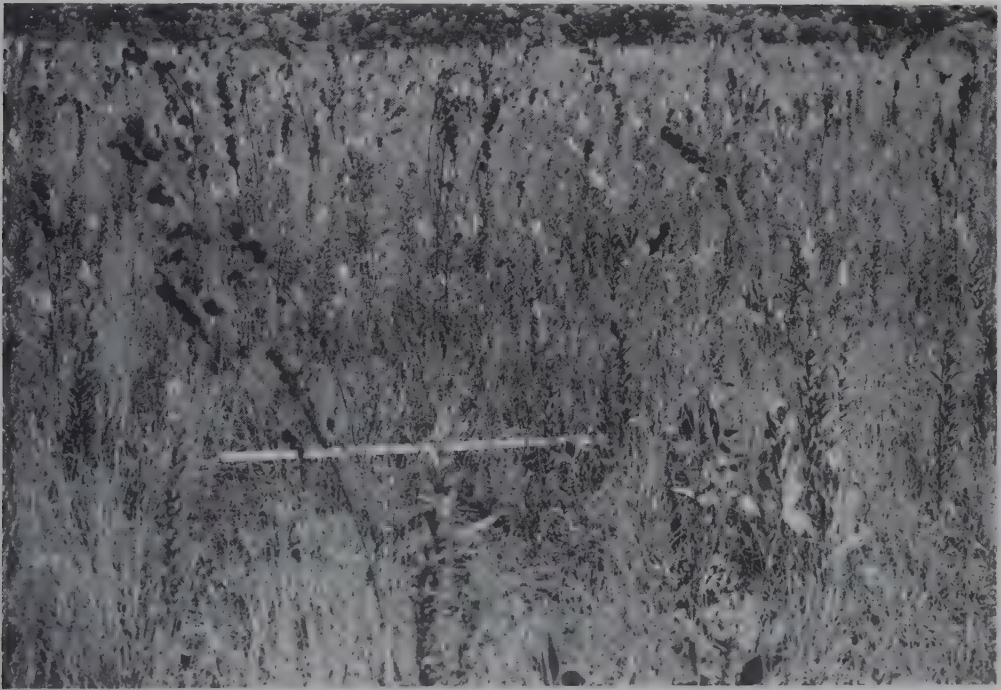

FIG. 5. *Aristida-Lespedeza* vegetation type, June 12, 1954. The bush-clover gains prominence in areas where the grasses are less dense. Photograph by E. B. Hazard.

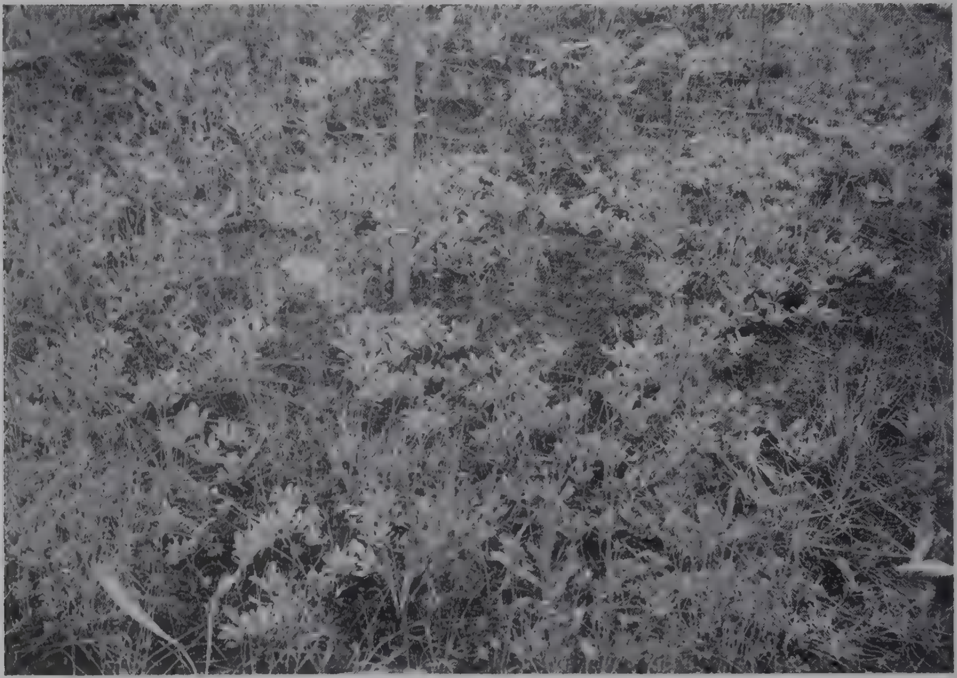

FIG. 6. Bryoid-*Antennaria* vegetation type, July 8, 1954. Pussy-toes, mosses and lichens dominate, and grasses are greatly reduced in importance. Photograph by P. J. R. Hill.

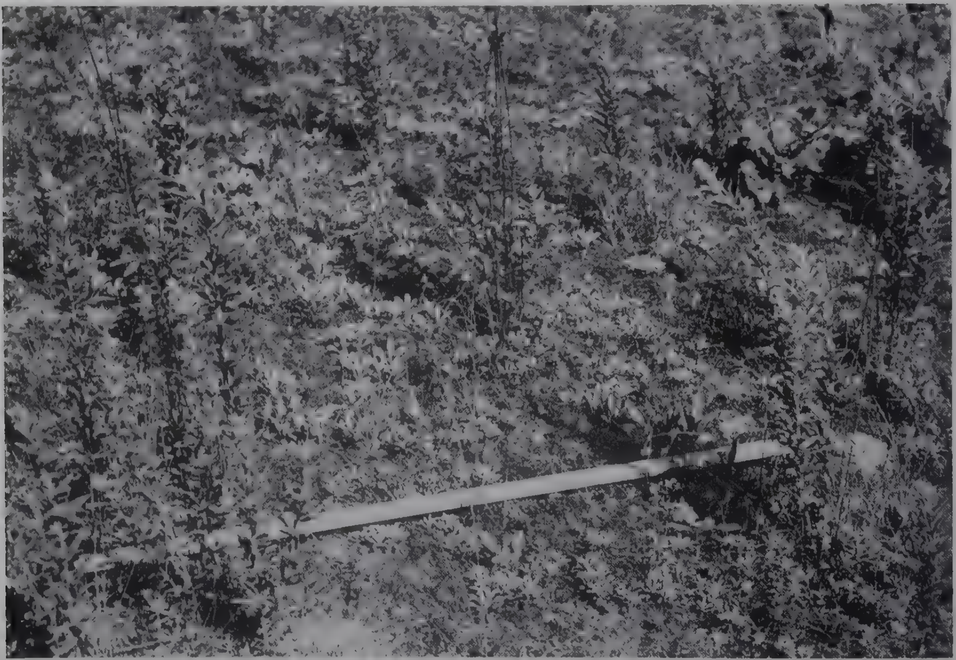

FIG. 7. Bryoid-*Antennaria-Lespedeza* vegetation type, June 12, 1954. The bush-clover does not grow densely enough to affect the well-developed ground stratum. Photograph by E. B. Hazard.

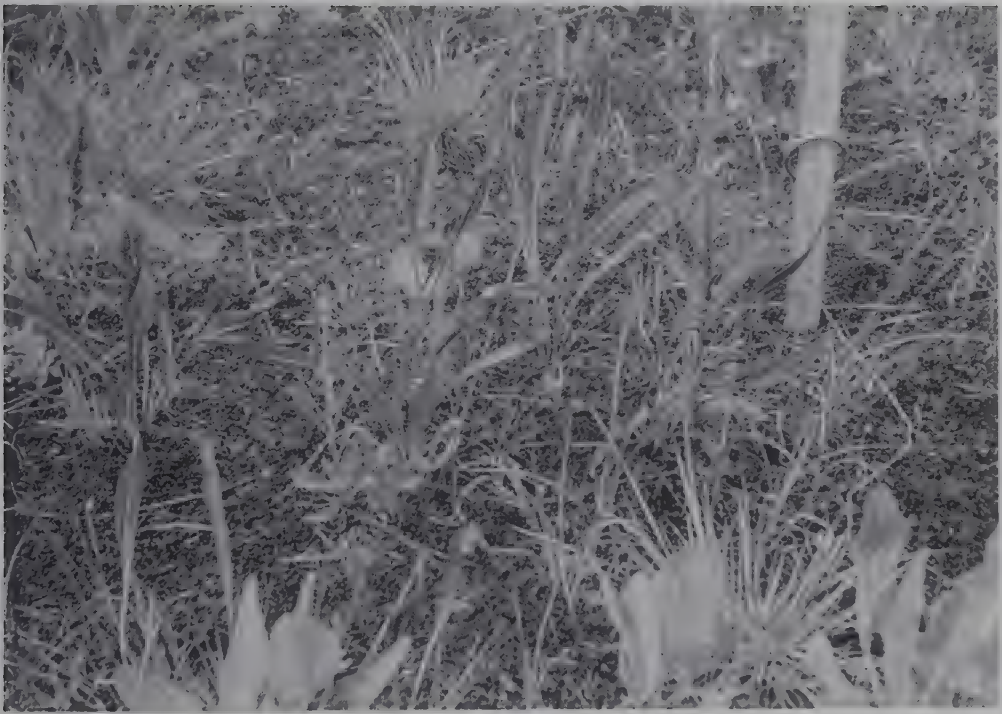

FIG. 8. Bryoid-*Antennaria-Liatris* vegetation type, July 8, 1954. Blazing star and panic grass may be locally conspicuous and produce a variant type of vegetation. Photograph by P. J. R. Hill.

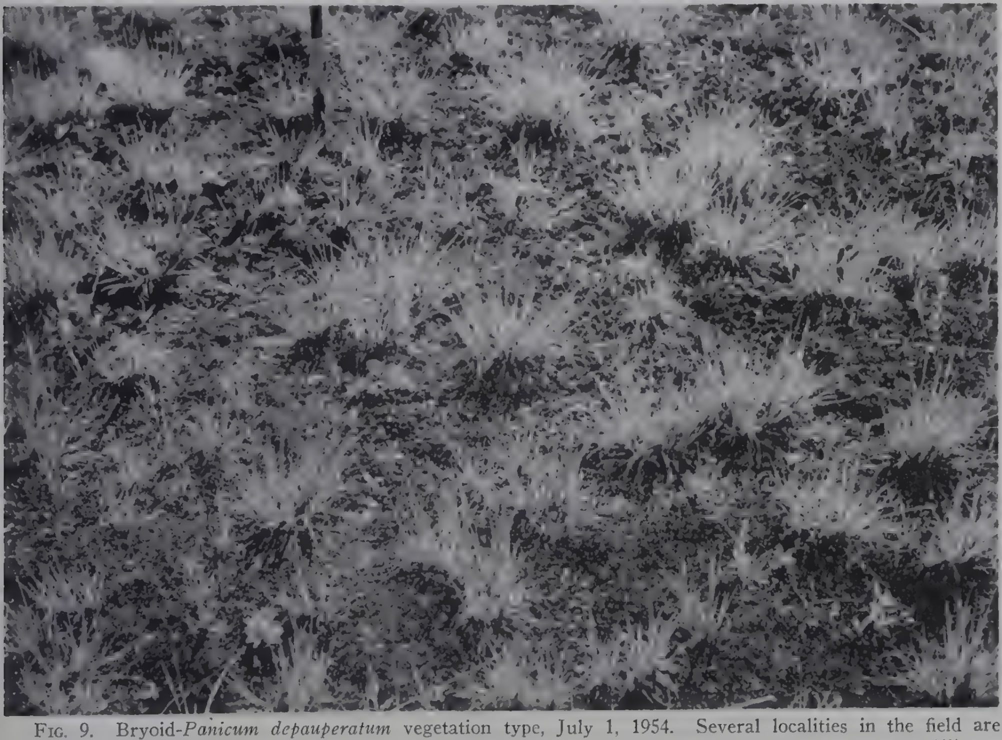

FIG. 9. Bryoid-*Panicum depauperatum* vegetation type, July 1, 1954. Several localities in the field are dominated by clumps of panic grass set in a matrix of mosses and lichens. Photograph by P. J. R. Hill.

(11-18). ND, usually high (4-11). Total species, 39.

Dominants: *Antennaria fallax**, *A. neglecta*, *Ceratodon purpureus*, *Polytrichum piliferum* Hedw.*, *Cladonia cristatella*.

Constants: *Aristida purpurascens*, *Poa compressa*, *Hieracium longipilum*, *Rumex acetosella*, *Solidago nemoralis*, *Cladonia clavulifera* Tuck.*, *C. pyxidata*, *C. nemoxyna*, *C. verticillata* Hoffm.*

Observed types: Four types were recorded. The Bryoid-*Antennaria* type proper (Type No. 6) is characterized principally by the high cover of *Antennaria* and the greatly reduced importance of other forbs and grasses. The Bryoid-*Antennaria Lespedeza* type (Type No. 7) is marked by the high cover and conspicuousness of *L. capitata*. A somewhat impoverished D stratum and the prominence of *Liatris aspera* characterize the Bryoid-*Antennaria-Liatris* type (Type No. 8). The Bryoid-*Panicum depauperatum* type (Type No. 9), has a well-developed ground stratum but the *Antennaria* cover is reduced and *P. depauperatum* dominates the C stratum.

Types of uncertain status

Two additional types are sufficiently distinct to warrant recognition, but their characteristics combine features of different Groups and in some respects cut across lines of differentiation between the two major subdivisions of the field vegetation.

Type No. 10. The *Leptoloma cognatum* type (Figure 10). *L. cognatum* (Schultes) Chase grows in clumps which are relatively widely spaced Under these conditions the two species of *Poa* establish themselves together. There is a weakly-developed lichen mat, but mosses are rarely encountered.

General characteristics: TC, high (80-100 per cent). TD, usually low but variable (0-50 per cent). TS, low (0-10 per cent). NC, medium (7-16). ND, usually low (2-6). Total species, 27.

Dominants: *Leptoloma cognatum**.

Constants: *Poa pratensis*, *P. compressa*, *Rumex acetosella*, *Oxalis stricta* L., *Cladonia cristatella*, *C. nemoxyna*, *C. pyxidata*.

Type No. 11. The *Solidago rigida* type (Figure 11). The dominance of this goldenrod markedly reduced the conspicuousness of grasses. There are a good many other species of forbs, but these are generally sparsely distributed. The ground stratum is fairly well-developed.

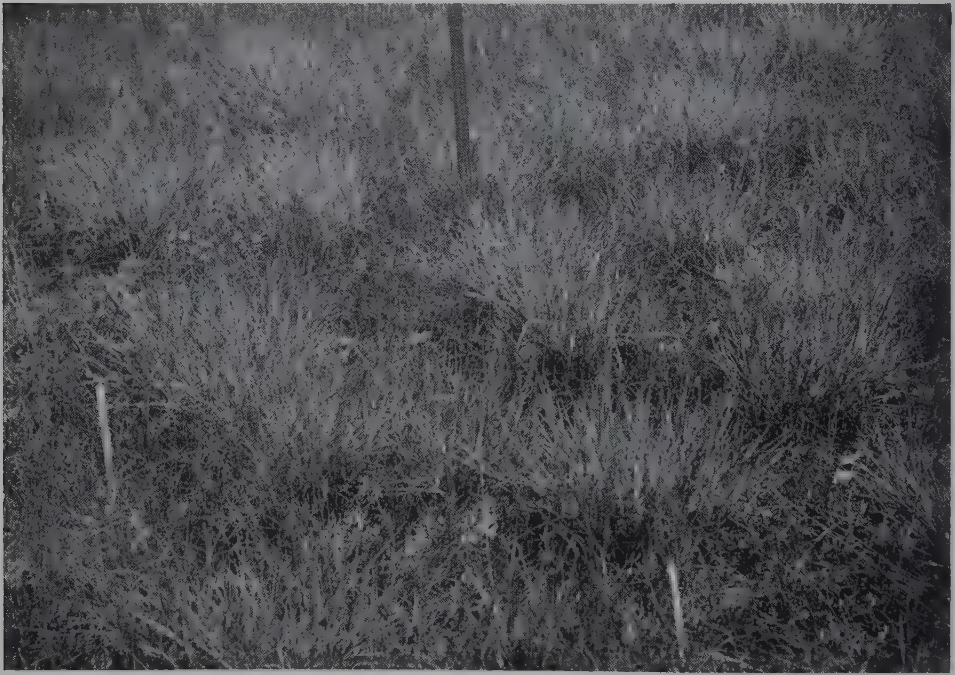

FIG. 10. *Leptoloma cognatum* vegetation type, July 8, 1954. Between the widely spaced clumps of this grass, both species of bluegrass occur together. Few mosses are found in this type. Photograph by P. J. R. Hill.

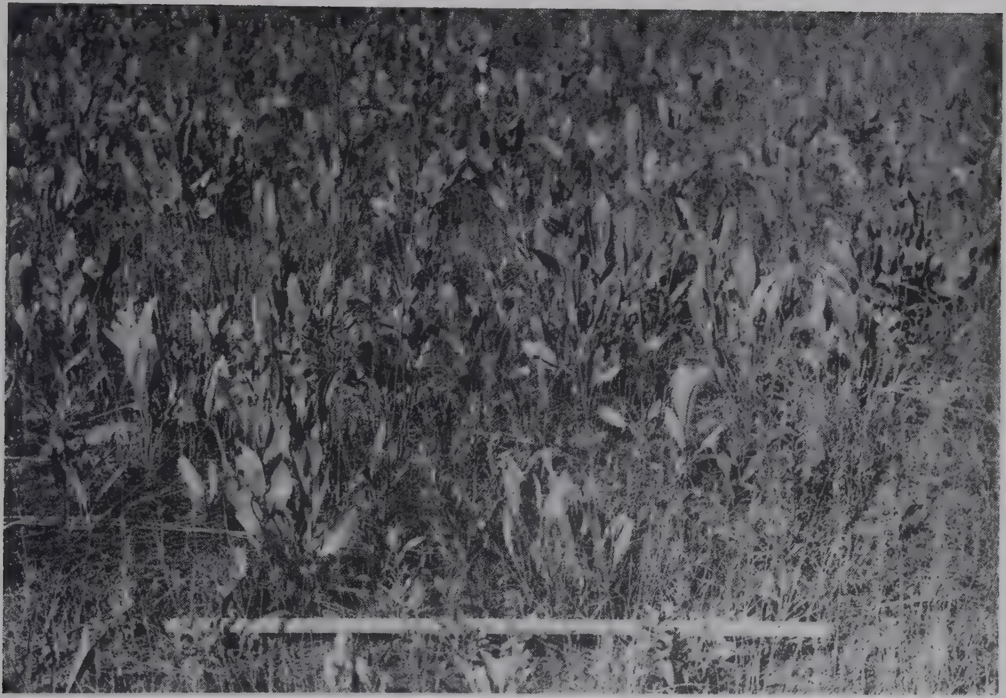

FIG. 11. *Solidago rigida* vegetation type, June 12, 1954. The high cover produced by the goldenrod brings about a decrease in the conspicuousness of the grasses. Photograph by E. B. Hazard.

General characteristics: TC, medium (40-70 per cent). TD, low (0-30 per cent). TS, low (0-10 per cent). NC, high (15-22). ND, medium (3-8). Total species, 38.

Dominants: *Solidago rigida* L.

Constants: *Poa compressa, Aristida purpurascens, Ambrosia artemisiifolia, Antennaria neglecta, Rumex acetosella, Solidago juncea, S. nemoralis, Cladonia cristatella, C. nemoxyna, C. pyxidata.*

MINIMAL AREA OF VEGETATION TYPES

The validity of descriptions of, and comparisons between, types of vegetation rests on the assumption that the size of the sample plots employed is large enough to permit the development of the characteristics of those types. As a test case for the present study, the 10 sample plots taken from type No. 4 (*Poa-Aristida*), which ranged from 4 to 10 m^2. and averaged 6.3 m^2., were examined for adequacy with respect to minimal area. In each of the ten sampled stands of this type, we also examined 1 quadrat of each of the following sizes: 0.01m^2., 0.04^2., 0.16m^2., 0.64m^2., and 2.56m^2. Each quadrat was completely independent of every other quadrat, and the entire procedure was carried out as randomly as possible. Table V records the frequency of occurrence of the various species encountered in the 10 quadrats of each size and in the 10 sample plots. There is a high degree of similarity between the two sets of data. Thirty-two species were common to both, 7 were recorded in the quadrats but not in the sample plots, and 6 were taken in the sample plots but not in the quadrats. All of the dominant and constant species of the sample plots were also found in the quadrat series and usually occurred with similar frequencies in the largest quadrats. Species which were exclusive to either the sample plots or the quadrats rarely occurred with a frequency of more than 10 per cent and were often represented by single individuals. The characteristics of the *Poa-Aristida* type seem to have been fully developed on quadrats of the 2.56m.^{2} size, *i.e.,* on considerably smaller areas than those selected for the type description. This type was selected for testing because it is one of the more variable types on the field. We conclude, therefore, that our plot sizes satisfy the requirements of minimal area.

COMPARISON OF GROUPS OF VEGETATION TYPES

The *Poa pratensis* Group of vegetation types can readily be distinguished by its visible char-

TABLE V. *Per cent frequency of occurrence of species in 10 random quadrats of increasing sizes, and in 10 sample plots in the* Poa-Aristida *vegetation type, old-field community, E. S. George Reserve, Livingston County, Michigan. October 23, 1953*

Species	Quadrats					Sample plots
	0.01 m²	0.04 m²	0.16 m²	0.64 m²	2.56 m²	4 m²-10 m²
Aristida purpurascens Poir.	90	100	100	100	100	100
Cyperus filiculmis Vahl	20	10	20	50	40	30
Danthonia spicata (L.) Beauv.	0	0	10	0	10	20
Leptoloma cognatum (Schultes) Chase	0	0	10	20	20	0
Panicum depauperatum Muhl.	10	0	0	10	60	60
P. lanuginosum Ell.	0	0	0	10	10	0
P. oligosanthes Schultes	0	10	30	60	50	30
Poa compressa L.	100	80	90	100	100	100
P. pratensis L.	20	20	20	30	40	0
Achillea millefolium L.	0	0	0	0	0	20
Ambrosia artemisiifolia L.	0	0	0	10	40	50
Antennaria fallax Greene	0	0	10	40	40	50
A. neglecta Greene	0	0	0	10	30	80
Desmodium illinoense Gray	0	0	0	10	0	0
Erigeron strigosus Muhl.	0	0	20	20	40	30
Euphorbia corollata L.	0	0	0	0	10	10
Galium pilosum Ait.	0	0	0	0	10	0
Gnaphalium obtusifolium L.	0	20	50	40	70	90
Hedeoma hispida Pursh	0	0	0	10	20	10
Hieracium gronovii L.	10	10	0	10	50	90
H. longipilum L.	0	10	20	60	90	100
Houstonia longifolia Gaertn.	0	0	0	0	0	10
Lactuca spp.	0	10	10	30	20	30
Lespedeza capitata Michx.	0	0	10	30	20	60
Liatris aspera Michx.	0	0	10	0	20	20
Oxalis stricta L.	0	10	10	30	30	40
Physalis heterophylla Nees	0	0	0	0	10	10
Polygonum tenue Michx.	0	0	10	0	0	30
Potentilla intermedia L.	0	0	0	0	0	10
P. simplex Michx.	0	0	0	0	0	10
Rumex acetosella L.	100	100	100	100	100	100
Solidago juncea Ait.	0	0	0	10	10	0
S. nemoralis Ait.	0	30	40	90	100	100
S. rigida L.	0	0	0	10	40	30
Tragopogon pratensis L.	0	10	20	30	30	50
Brachythecium sp.	0	0	0	0	0	10
Ceratodon purpureus (Hedw.) Brid.	10	20	40	60	70	80
Polytrichum juniperinum Hedw.	0	0	0	0	10	0
P. piliferum Hedw.	0	0	0	10	30	40
Cladonia cristatella Tuck.	90	100	100	100	100	100
C. nemoxyna (Ach.) Coem.	30	60	80	100	100	100
C. pyxidata (L.) Fr.	10	20	60	60	100	100
C. verticillata Hoffm.	0	10	20	0	10	10
Lecidea granulosa (Ehrh.) Ach.	0	0	0	0	0	10
Peltigera spuria (Ach.) DC.	0	0	0	20	0	30
Total species	11	18	24	31	36	38

acteristics which have been described above. Frequent observations since 1948 have shown that the boundaries between the *P. pratensis* types and the rest of the vegetation are always well-defined and constant from year to year.

The 3 Groups of upland types, however, frequently give way to each other very gradually, and the differences among them are less obvious. The *Poa compressa* Group, by virtue of its homogeneous appearance and feeble ground stratum, is the most distinct of these. It seems to represent a phase of the upland vegetation in which *Aristida* has been suppressed as a dominant. The *Poa-Aristida* Group is regarded as the typical upland phase of the field, with both the C and D strata well-developed and with richer flora than either the *Poa compressa* or the Bryoid-*Antennaria* Group. The latter is distinguished by the suppression of both *Poa* and *Aristida* as dominants, by the sparseness of the C stratum and the prominence of the ground vegetation. In the Bryoid-*Antennaria* types, mosses generally dominate over lichens, whereas in the *Poa-Aristida* types the reverse is usually the case. The Bryoid-*Antennaria* Group is also the most variable of the upland Groups.

Floristic relationships among the 4 Groups of vegetation types were also evaluated by applying Sörenson's (1948) index of similarity, in which two types can be compared by the formula:

$$I_s = \frac{2c \times 100}{a + b}$$

where a represents the number of species found in one type, b the number of species found in the other type, and c the number of species common to both. This formula has been applied to the data obtained from the sample plots, as given in Table III, with the following results:

Group comparison	Index of similarity
Poa pratensis vs. Bryoid-*Antennaria*	38
Poa pratensis vs. *Poa-Aristida*	48
Poa pratensis vs. *Poa compressa*	58
Poa compressa vs. Bryoid-*Antennaria*	60
Poa compressa vs. *Poa-Aristida*	71
Poa-Aristida vs. Bryoid-*Antennaria*	78

The *Poa pratensis* Group has less floristically in common with the Bryoid-*Antennaria, Poa-Aristida,* and *Poa compressa* Groups than these have with each other. This tends to support the hypothesis of a greater degree of vegetational differentiation for the *Poa pratensis* Group. Of the 3 upland Groups, *Poa compressa* has the most distinct flora, and *Poa-Aristida* and Bryoid-*Antennaria* share the greatest percentage of species. Similar comparisons between the various Groups and the *Leptoloma cognatum* and *Solidago rigida* types indicate that the former has its greatest floristic affinities with the *Poa compressa* Group, whereas the latter is most closely allied to the *Poa-Aristida* Group.

Relations of Vegetation Types to Environmental Factors

It is probable that the position of seed sources, the direction of the wind, and other "chance" factors in determining what species reach and colonize a given locality have played a considerable part in the creation of the vegetation pattern of the field. These factors cannot be readily evaluated, however, and are less likely to exhibit clear relationships to the present distribution of the different vegetation types than are the more obvious and proximate features of physiography and soil. We now consider briefly some of the broad aspects of environmental relations which bear on the problem of the local distribution of types.

Topography

The distribution of the *Poa pratensis* vegetation types on the field is clearly limited to the basin-like depressions. Despite their shallowness, these basins are sufficiently developed to create distinct microclimatic conditions, as shown by the data of Table VI. Subsurface temperatures in the depressions tend to be higher in the winter and lower in the summer, and to change less rapidly, than those on the uplands. Snow cover accumulates to a greater degree and lasts longer in the depressions, and the soil is not frozen to so great a depth. Probably of greater importance to the vegetation, however, are the accumulation of soil particles and the moisture added by drainage from the higher levels. A partial profile of one of the depressions is illustrated in Figure 12. It should be noted that the *Poa pratensis* types are closely restricted to the surface accumulation of silt loam which has filled the basin bottom.

Table VI. *Soil temperatures in °F. taken at a depth of 1.5 inches, and depth of frozen soil in inches (in parentheses), in upland and depression sites in an old-field community, E. S. George Reserve, Livingston County, Michigan, September 1949-September 1950. From data taken by Nelson G. Hairston*

Date	Upland sites	Depression sites	Date	Upland sites	Depression sites
September 22..	64	61	March 25.....	36	32
October 20....	66	62	April 8.......	44	36
October 27....	51	50	April 29......	50	42
November 10..	51	50	May 6.......	58	51
November 17..	44	44	May 20......	69	65
December 1....	32	33	June 10......	78	75
December 15...	28 (2.5)	30 (1.0)	June 24......	81	77
December 29...	33	34	July 15.......	75	74
January 19....	26 (8.0)	31 (3.0)	August 19....	71	72
February 1....	32	32	August 26....	74	69
February 18...	32 (3.0)	32 (1.5)	September 2..	68	64
March 15......	33 (8.5)	32 (5.0)			

Topographic features could not be so definitely associated with any other of the vegetation types. There was a tendency for the *Leptoloma cognatum* type to occur on slopes rather than in the de-

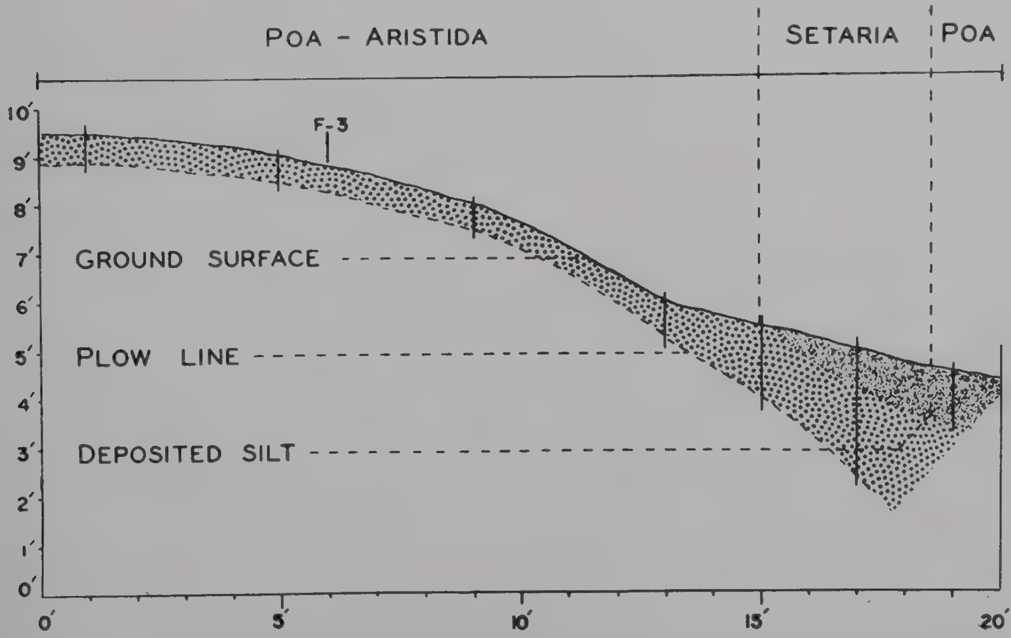

Fig. 12. Profile of slope westward from grid marker F-3 into depression, showing relations of vegetation types and surface soils, in an abandoned field, E. S. George Reserve, Livingston County, Michigan, constructed by F. C. Evans and E. Dahl, October 16, 1953. Solid vertical lines indicate locations of sample soil profiles.

Table VII. *Soil texture and pH analyses of samples from vegetation types of an old-field community and from sites in an adjacent oak-hickory woods, E. S. George Reserve, Livingston County, Michigan. Samples contained 50 grams of material after removal of gravels; starred samples contained 100 grams. Particle sizes are as follows: gravels, larger than 2.0 mm.; sands, 2.0-0.05 mm.; silts, 0.05-0.002 mm.; clays, less than 0.002 mm. Unless otherwise noted, samples were taken at a depth of 2-7 cm.*

Sample type	pH	Per cent of total sample	Per cent of sample after removal of gravel			Textural class
		gravel	sands	silts	clays	
Poa pratensis	5.5	1.4	25.4	56.8	17.8	silt loam
Setaria glauca	5.5	14.2	67.8	20.4	11.8	sandy loam
Poa compressa	5.5	9.1	76.4	14.6	9.0	sandy loam
Poa compressa*	6.0	11.2	79.9	13.1	7.0	sandy loam
Bryoid-Antennaria	5.5	17.4	76.4	14.2	9.4	sandy loam
Bryoid-Antennaria-Liatris	5.5	6.0	76.4	14.8	8.8	sandy loam
Bryoid-Antennaria-Lespedeza*	5.0	13.2	80.1	12.7	7.2	sand
Byroid-Panicum depauperatum*	5.5	17.1	80.2	13.3	6.5	sand
Bryoid-Antennaria*	5.0	5.6	83.0	11.3	5.7	sand
Aristida-Lespedeza*	6.0	16.0	82.0	10.1	7.2	sand
Poa-Aristida*	5.5	19.1	84.0	9.2	6.8	sand
Poa-Aristida*	5.5	13.1	90.0	6.1	3.9	sand
Leptoloma cognatum*	6.0	10.8	79.2	14.1	6.7	sandy loam
Solidago rigida	5.0	2.7	40.2	40.6	19.2	loam
(a) Woods, level upland	6.5	3.6	69.4	20.6	10.0	sandy loam
(b) Woods, kettle hole not receiving drainage from field	6.5	0.7	75.4	15.4	9.2	sandy loam
(c) Woods, kettle hole, drainage from field	6.0	0.0	18.4	60.4	21.2	silty clay loam
(d) Like c, depth 20-25 cm.	6.0	0.0	9.4	58.8	31.8	silty clay loam
(e) Like c, depth 31-36 cm.	6.0	2.0	73.8	13.6	12.6	sandy loam

pressions or on the uplands, but it was impossible to differentiate the other types on the basis of localized relief characters.

Soil texture

Marked differences in texture among the soils from the various types were revealed by mechanical analyses, the results of which are shown in Table VII. The *Poa pratensis* soil contained virtually no gravel and was comparatively low in sands and high in silts and clays. In the *Setaria* type, only a few feet away from but slightly above the *Poa pratensis,* there was a definite increase in the amount of gravel and in the percentage of sands, sufficient to classify the soil as sandy loam. The soils of the *Poa compressa,* Bryoid-*Antennaria* and *Poa-Aristida* types can be arranged in a series showing increasing amounts of sands and corresponding reductions of the finer fractions, and the Bryoid-*Antennaria* and *Poa-Aristida* soils generally fall into the textural class of sands. Soil from the *Leptoloma cognatum* type is texturally most like that from *Poa compressa,* and the *Solidago rigida* type soil is *quite* similar to that from the *Poa pratensis* types.

Soil acidity

Records of pH in the samples from the various vegetation types are also shown in Table VII. Although they indicate the general level of acidity in the surface soils of the field and suggest a slightly more acid condition than in the adjacent woods, they permit little in the way of conclusions about the distribution of types. In general, differences in soil acidity show no correlation with the distribution patterns. More critical measurements made with a glass electrode gave a mean pH value of 5.70 for a series of 5 samples from the *Poa-Aristida* type and one of 6.28 for a series of 5 samples from the *Poa compressa* type. The difference is statistically significant ($t = 2.73$, $d.f. = 8$, $p. < .05$). *Poa compressa* thus seems to be associated with slightly less acid soil than that on which *Poa-Aristida* occurs.

Depth of plow line

The discontinuity between the upper brown sand (the A_p horizon) and the lower, paler material of the Fox sandy loam is generally considered to represent the plow line. The depth to this line was measured in each of the sample plots studied; the ranges of plot values and the average depth for each type are given in Table II. At the edges of the depressions the plow lines tend to be buried (Figure 12) and it is not known whether the depressions themselves were ever plowed. For the upland vegetation types, the measurements of depth to plow line were subjected to an analysis of variance. Although there was considerable variation in depth within each type, there were highly significant differences in mean depth between types ($F_{6,\,36} = 3.729$, $p. < .01$). Ten of the 21 possible comparisons of mean depth yielded significant differences at the 5 per cent level when evaluated by the Student-Fisher t test. The *Poa compressa* type differed from all of the 4 Bryoid-*Antennaria* types, both of the *Poa-Aristida* types differed from the Bryoid-*Panicum depauperatum* and Bryoid-*Antennaria-Lespedeza* types, and the 2 latter types differed from the Bryoid-*Antennaria-Liatris* type. The distribution of the various vegetation types, therefore, appeared to be associated with the depth of the soil material lying above the plow line.

Water economy

No measurements were made of the water content or capacity of the soil samples from the vegetation types. The association of these types with differences in topographic relief and with soil differences suggests, however, that water relations may also be important. Although water does not stand for any appreciable period on any part of the field, even in the depressions, the subsurface moisture in the *Poa pratensis* areas is almost always perceptibly greater than on the uplands. It is quite possible that soil moisture is a more important limiting factor than soil texture in the distribution of the *Poa pratensis* vegetation type. On the uplands, however, local differences in soil moisture must be very slight and are less likely to account for vegetational variation.

Effect of trees

The *Poa compressa* type was best expressed at the margins of the adjoining woods and in the immediate vicinity of the several large hickory (*Carya ovalis* (Wang.) Sarg.) trees left on the field by the early settlers. *P. compressa* also occurs as a regular component of the oak-hickory floor stratum and is apparently quite tolerant to shade (which here implies interception of precipitation as well as reduced light) and to other effects of trees, such as intense root concentrations and deposition of litter. The presence of these trees may tend to eliminate such open field species as *Aristida purpurascens* and thus permit *P. compressa* to achieve sole dominance.

Ground litter

The several types differed considerably in the amount of litter present. Very little tends to accumulate in the Bryoid-*Antennaria* types; such as there is does not form a dense cover, and the dead stems of grasses and forbs remain more or less upright throughout much of the year following that of their growth, unless they are broken off sooner and blown away. This is also true of the *Poa-Aristida* types. In contrast, the *Poa compressa* type, as previously indicated, usually has a conspicuous mat of partially decomposed culms. The growth habits of this grass also seem to favor the accumulation of tree leaves. Leaves of *Carya* and *Quercus* were generally abundant in *P. compressa* litter but did not collect in the other vegetation types. This might account in part for the higher pH values in the *P. compressa* soils and suggests a local increase in the concentration of salts, since there is often, in regions of podzolization, an association between high pH and high nutritional levels.

The Influence of Previous Cultivation

It seemed probable that the differences in soil texture and in depth to the plow line were due to former cultivation practices and to subsequent differential erosion and deposition. Plowing procedures of 50 years ago were apparently not very different from those of today in southeastern Michigan. We are informed by A. J. Bell, Department of Agricultural Engineering, Michigan State University, that the older plows were somewhat narrower (usually 10-12 inches wide) and that in 1900 some of them still had wooden beams, although steel beams had become quite common in this part of the country. They produced contiguous furrows which averaged 12-15 cm. in depth in soils of a sandy type, thus cutting not quite so deeply as present-day plows. To evaluate the effects which cultivation may have had upon the soils of the field, a series of soil samples were taken in the oak-hickory woodlot lying adjacent to the west, where the ground had not been disturbed by plowing. Analytical data for these samples are given in Table VII. In this woodlot, the ground was covered with a litter of dead leaves of the forest trees forming a layer several centimeters deep. Beneath this was a thin (1-2 cm.) layer of humus, permeated with fungal hyphae, which was readily separable from the underlying layer. The latter was somewhat humified to a depth of 8-10 cm., but there was no sharp discontinuity between the humified horizon and the material beneath. Instead, it gave way gradually to a leached, yellow-brown sandy loam much like that at a corresponding depth in the field. The deeper horizons of the soil profile in the woods did not differ essentially from those in the field. However, the litter and humus of the woods tended to intercept rainfall and to prevent rapid percolation. When rain fell after a period of drought, therefore, the subsurface materials in the woods were usually drier than those of the field. Woods soils from level upland sites (*cf.* Table VII, sample a) comparable to those on the field contained a smaller percentage of sands and a higher percentage of silts and clays. This probably represents the condition of the upland soils on the field prior to removal of the tree cover. Disturbance of the field soil through plowing and subsequent erosion has apparently resulted in the removal of some of the finer fractions from the A_p horizon in the higher areas of the field, leaving a relatively greater proportion of coarser materials.

Further evidence of the influence of previous cultivation was secured from examinations of the soil of depressions in the woods, where eroded material might be expected to accumulate. A soil sample taken in a kettle hole sufficiently remote from the field not to receive drainage from it (Table VII, sample b) was very much like the upland woods sample, indicating that there is relatively little erosion within the woods, probably because the abundant leaf litter not only affords mechanical protection but also reduces the volume of precipitation reaching the surface of the mineral soil. In contrast, a sample taken in a kettle hole at the edge of the woods next to the field (Table VII, sample c) showed a great increase in silts and clays and a decline in the proportion of sands. This difference was even more marked in a deeper sample from the same site (Table VII, sample d). The finer-textured soil continued to a depth of 30 cm. and then gave way abruptly to coarser material which (Table VII, sample e) gave a fractional analysis much like those from undisturbed woods soil (samples a and b). Examinations of soil profiles in other kettle holes and in other woodlots adjacent to the field gave similar results. All of this evidence seems to indicate that appreciable erosion has occurred in the field and that some of the eroded material has been deposited in the field depressions and some of it has been carried off into adjacent basins.

There is also evidence that some erosion is still taking place on the field. Evans and Cain (1952) noted the occurrence of numerous small erosion pavements and the exposure of corms of *Cyperus filiculmis* Vahl and of normally buried parts of *Antennaria* and other forbs. Phenomena of this sort are most apparent in the Bryoid-*Antennaria* types, which are characterized by considerable amounts of bare soil. Run-off channels can sometimes be seen on the slopes leading to the depressions. The rate of erosion at the present time, however, seems to be very low and to have little effect on the existing pattern of vegetation.

Integration of Vegetation Types in the Community

The vegetation types in the field are evidently the result of diverse responses to numerous factors. Our conception of the environmental relationships among the various types is illustrated diagrammatically in Figure 13. Topographic relief, through its control of drainage, silt accumulation, and microclimate, is apparently responsible for the major subdivision into upland and depression types. On the upland areas, differential erosion seems to be the principal factor influencing type distribution. The *Poa-Aristida* types are given a central position as representative of stabilized upland conditions, whereas the Bryoid-*Antennaria* types are found where the soil is exposed and shifting. Variations in ground litter, nutritional level of the soil, and soil acidity are probably of secondary importance. The occurrence of trees, giving rise to increased shade and perhaps to other effects as well, seems to favor the *Poa compressa* type. The positions of the *Leptoloma cognatum* and *Solidago rigida* types are less certain, but the former seems to lie between the *Poa pratensis* and *Poa compressa* types and the latter appears

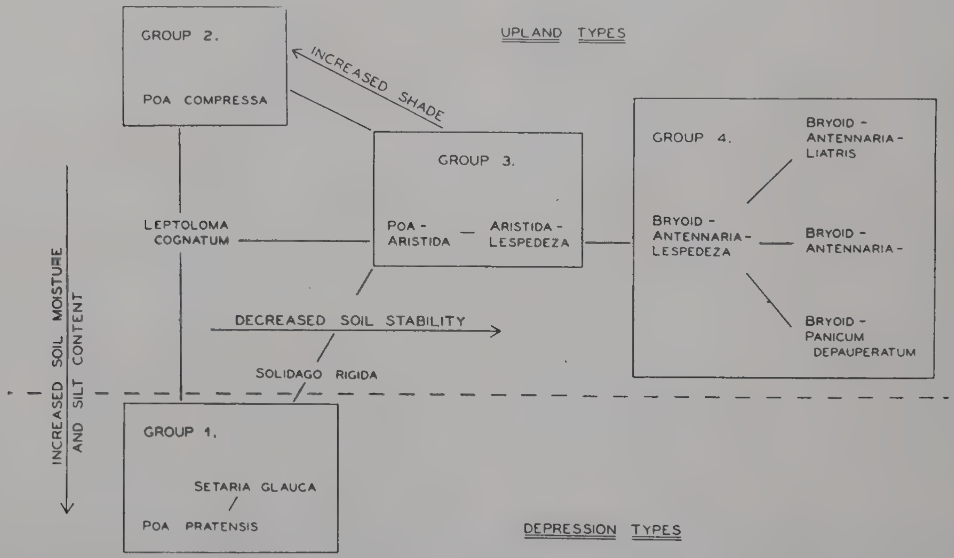

FIG. 13. Diagrammatic scheme of relationships among vegetation types and environmental factors in an abandoned field, E. S. George Reserve, Livingston County, Michigan. F. C. Evans and E. Dahl, October, 1953.

to be intermediate between the *Poa pratensis* and *Poa-Aristida* types.

The concept of localized response to environmental variation is of course implicit in most descriptions of regional vegetation but it is not always recognized in small-scale situations. Each of the environmental factors which seem to have influenced the vegetational pattern of the field can be presumed to have a distribution of its own, the net effect of which has been to create a number of distinctive minor habitats. Each such minor habitat has its unique constellation of forces which have acted selectively on the plants reaching it. Some of these forces, such as erosion, have undoubtedly been operative throughout the entire period of more than 50 years during which the revegetation of the field has been taking place. Others, resulting from the presence of those plants and animals which have succeeded in establishing themselves in these minor habitats, are of more recent origin. With the passage of time, the intensity of selective action has probably not remained constant for any of the factors involved but has either decreased or increased. The mosaic structure of the existing vegetation reflects not only the current degree of adjustment to the immediate environment but also the history of adaptation to past selective pressures.

Very little change has been noted since 1948, when the plant cover of the field was first studied. In the absence of further human intervention, alteration of the local topography can be expected to proceed very slowly. The present vegetation inhibits extensive erosion and there is evidence that surfaces which were once subject to more rapid removal of soil are now fairly well stabilized. Remnants of Bryoid-*Antennaria* types can frequently be found in vegetation that is clearly of the *Poa-Aristida* type, suggesting that the latter tends to supplant the former as the stability of the soil surface increases. Shifts of this sort will undoubtedly create slight modifications in the over-all pattern of vegetation, but it seems likely that, barring such catastrophes as fire, any major alteration of the latter must await the establishment and dominance of other species in the course of succession. Despite a half-century of abandonment, shrubs and arborescent species have not as yet markedly influenced the appearance of the field, which is clearly that of grassland. *Juniperus communis* L., *Crataegus* spp. and *Prunus serotina* Ehrh. occur only as sparsely distributed individuals, and invasion by *Quercus velutina* Lam., *Carya ovalis* (Wang.) Sarg. and other woods species is not apparent except at the extreme margins. The present balance between the vegetation types of the depressions and those of the upland areas seems likely to endure for some time, and although local adjustments may continue to be made the field vegetation as a whole appears to have attained a considerable degree of equilibrium with the environment.

SUMMARY

1. The vegetation of a 50-year-old abandoned field in southeastern Michigan was analyzed from a series of 65 selected sample plots. The floristic composition, estimates of plant cover, and characteristics of the surface soil were recorded for each plot.

2. Two major subdivisions of the field vegetation were recognized: (a) that of the shallow, basin-like depressions, dominated by a dense growth of *Poa pratensis,* and (b) that of the upland areas, dominated by *Poa compressa* and *Aristida purpurascens*. Eleven vegetation types of lesser magnitude, characterized in terms of dominant, constant, and differential species, were also identified. Phytosociological analyses of each type were made and used as the basis of diagnostic descriptions.

3. A study of species-area relationships in the *Poa-Aristida* vegetation type, used as a test case, suggested that the plot size (4-15m^2) employed for description of types satisfied the requirements of minimal area.

4. Nine of the types were classified into one depression and three upland Groups. Indices of floristic similarity were used to compare Groups, and the floristic distinctness of the depression (*Poa pratensis*) Group was substantiated.

5. Topographic variability was considered to be primarily responsible for the major vegetational subdivisions. The vegetation of the depressions was found to occur on silt loams, that of the upland areas on sandy loams and sands. Significant differences between the types in respect to soil texture and in depth to the plow line were also demonstrated.

6. Comparison of the field soils with undisturbed soils from the adjacent woods supported the hypothesis that the differences among the field soils were due to the effects of clearing and plowing, followed by differential erosion.

7. The over-all pattern of the plant cover was visualized as resulting from the interspersion of minor habitats, each with its own constellation of selective forces. There was little evidence of current change in pattern, and it was concluded that the field vegetation has attained a considerable degree of equilibrium with the environment.

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SOME ASPECTS OF HABITAT SELECTION AND OTHER[1] BEHAVIOR OF CAVERN-DWELLING BATS

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INTRODUCTION

The primary problem of bats is the conservation of energy. This is achieved through metabolic economy which is made possible through the universal chiropteran characteristic of a "poor" temperature regulating system. When flying, bats behave as homiothermic animals and can, therefore, travel long distances; but when resting, their body temperatures tend to approximate that of the environment. For this reason they have been termed heterothermic mammals (Hock 1951).

The wing membranes of bats, when expanded, increase the surface area so that the area per unit volume from which heat is lost is much greater than in any other mammal. This implies a very high metabolism if a high body temperature is to be maintained. The resting position of a medium-sized bat reduces this surface area-volume ratio about four and one-half times since the wing membranes are folded against the sides of the body which gives the bat about the same surface area-volume ratio as any other small mammal of the same weight. The metabolic demands of bats, then, are much reduced when they are resting. Even so, if bats maintained high body temperatures when resting as they do when flying, they would not be able to go for long periods of time without food since food reserves would be quickly catabolized despite the decreased surface area-volume ratio. If a population of bats is to maintain itself, it appears that one of the most important factors is the selection of proper habitat in which to rest. Conservation of energy, then, is largely achieved through physiological reactivity in relation to habitat selection.

Bats seem to have different metabolic requirements at different seasons of the year. Those bats that hibernate throughout the winter in temperate regions must rest in cold places so that the body metabolism is very low in order not to utilize the food reserves before the beginning of the next feeding season. In the feeding season, bats must rest in places warm enough so that digestion and assimilation may proceed. When bats begin to go into hiberation in the fall and when they begin to come out of hibernation in the spring, the problems of metabolism are those of resting in warm places after having eaten and resting in cold places when food is scarce. Resting bats, then, if they are to conserve their energy, must rest in habitats whose temperatures are suited to their metabolic needs.

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[1] Presented as a part of a doctoral dissertation at the University of Michigan. I am pleased to acknowledge the assistance of the members of my doctoral committee consisting of Marston Bates, Chairman; Dugald E. S. Brown; William H. Burt; Pierre Dansereau; Francis C. Evans; and Claude W. Hibbard, all of whom made many helpful suggestions regarding the preparation of the manuscript. Frederick E. Smith, also of the University of Michigan, was of much help in respect to statistical interpretation of the data and the preparation of the manuscript. Janet A. Twente aided in every aspect of the preparation of the manuscript including the drawing of most of the figures. She also assisted in gathering field data in December, 1953. Herbert C. Asel and Thane S. Robinson, of Lawrence, Kansas, also aided in gathering some of the field data.

The cooperation of the land-owners in the region studied was wholehearted and was essential to the completion of the problem. I would especially like to thank Mr. and Mrs. John McMoran of Coldwater, Kansas, for their many kindnesses. Mr. and Mrs. Dewey Merrihew of Alva, Oklahoma, Mr. and Mrs. Doyle Heft, and Mr. and Mrs. James Thompson of Coldwater, Kansas, all generously donated living quarters.

It has been often stressed that bats are unique among mammals in that they are the only group which has achieved flight. A uniqueness that is not frequently appreciated, however, is that although of small size, most bats have a phenomenally low reproductive potential. A few species of cave bats have two young per year although most have only one. This low reproductive potential implies a relatively long life and thus basic behavior differences from animals with a high reproductive potential. The problems confronting a population of small mammals having a high reproductive potential are those of limiting the size of the population. This is often accomplished through density-dependent behavior factors (Calhoun 1952; Brown 1953). The problems confronting a population of small mammals with a low reproductive potential such as bats, however, seem to be maintenance rather than limiting of size. In such populations, behavior interaction between individuals is relatively simple and passive; social behavior seems to keep the population at a high level with mutual benefit to all members. The opposite is the case in populations whose numbers are limited by density-dependent behavior factors where aggressive behavior favors only certain individuals. It is not surprising that dominance hierarchy and territoriality are, as a rule, lacking among bats in which, it will be shown, social aggregations aid in combating environmental stresses even when all of the members of these aggregations are in a torpid state. The interactions between bats are not the sort that limit population size, but rather they aid in the survival of all of the individuals.

Many bats are characterized by a type of social behavior that is unique among mammals. This is the formation of dense clusters of many individuals. Some bats cluster at all seasons of the year whereas others cluster only when lactating. It will be shown that the function of clusters in the winter is somewhat different from that of the summer. In the winter, when a low body temperature is advantageous to metabolic conservation, clustering serves to keep the bats cold. In the feeding season, a higher body temperature is necessary in order that digestion and assimilation may efficiently proceed. At this time, the clusters serve to conserve heat and to keep the body temperatures of the bats higher than that of the environment. The differences of cluster function at the various seasons are determined by the behavior of the bats within the clusters. This behavior, in turn, is governed by the temperature at the place the cluster has formed. The seasonal behavior of bats in clusters, then, is a function of the rate at which the bats have been metabolizing.

The hypothesis that the social behavior of clustering tends to aid in the survival of all members of a population can possibly be explained on the basis that bats have a low reproductive potential, are of small size, and go for long periods of time without food. Conservation of energy would therefore be of utmost importance to the survival of bats. The waste of energy involved in active behavior interaction between individuals would not be metabolically economical. Most of the yearly mortality, which cannot exceed 33 or 50 per cent in the bats studied, can probably be attributed to predation (Twente 1954a, 1955). It is suggested, then, that the population density of bats is not limited by density-dependent behavior factors.

The literature on the ecology and behavior of bats is scattered and voluminous, but it is primarily in the form of short notes and much of the data is not usable for this study. There have been no attempts to analyze the behavior of bats in selecting habitat or to study the effect of the environment on the behavior of the animals.

This study was undertaken to establish the relationship of poor temperature control and metabolic conservation to habitat selection and the accompanying behavior. An effort was made to ascertain the habitat requirements of different species of bats and behavior utilized by the bats in the selection of this habitat.

Since bats are mobile creatures, they can fly great distances to find suitable habitat. This habitat, however, is discontinuous for most species of bats in the temperate zones. Underground passageways offer a suitable environment which is cold in the winter and yet not freezing. Even within these underground passageways, however, microclimatic conditions vary so that the selection of habitat within them must take place. It has been found in this study that bats have both active and passive means of selecting habitat suitable to their metabolic needs.

The small gypsum caverns in south-central Kansas and northwestern Oklahoma, with which this paper is concerned, offer an ideal situation for studying behavior and habitat requirements of four genera of vespertilionid bats. These genera are Myotis, Corynorhinus, Antrozous, and Eptesicus.

Caverns may be distinguished from caves in that caves have but one entrance whereas caverns have two or more entrances. Caves tend to maintain the same temperature throughout the year. Temperatures in caverns, on the other hand, are variable in that the two openings allow for air circulation and thus for microclimatic fluctuation. A study of habitat selection in caves would seem to be less illuminating than in caverns for the reason that there is less environmental fluctuation in caves. The differences of habitat between caverns and within a single cavern offer variable situations to be selected by bats. This would not be the case in the more constant conditions of caves. The responses of the bats to the changing environmental conditions, then, would seem to give a clearer picture of environmental influences than in the more constant conditions of caves.

The four genera of bats studied, due to different behavior patterns, seem to select somewhat different types of habitat in which to rest, but the type selected by each genus seems to serve the same end in providing proper environment for the metabolic needs of the bats. The resting places within the caverns that are selected by each genus are determined partly by climatic conditions, partly by the morphological characteristics of the walls and ceilings, and partly by a social tendency to form close aggregations. The distribution of all species may overlap, but generally it can be said that the type of habitat selected by each species is different.

The problem of habitat selection was attacked by observation of the animals and physical measurements of the environment in which they were found. A study of the microclimate at the places bats are found shows the environmental conditions that they select. It will be shown that in the winter the length of time a bat remains in one place is indicative of the effectiveness of the type of habitat selection utilized.

Bats were weighed throughout the winter and weight losses calculated to relate the temperatures of the places selected for hibernation to the amount of stored food catabolized. This gives an indication of the comparative effectiveness of the various types of habitat selection utilized by the different bats.

Since the habitat-selection behavior of bats seems to be one of the most important factors in the survival of the species, and since the body temperature, and thus the metabolic rate, of resting bats is dependent upon the temperature of the environment, except where modified by the social behavior of clustering, it would appear that through a study of habitat selection and clustering the effect of environmental stresses on the behavior of bats can be best understood. In short, this is a field study of the behavioral reponses of four genera of bats to changing environmental conditions.

The Bats

The bats with which this study is concerned are: *Myotis velifer incautus* (J. A. Allen), the cave Myotis; *Corynorhinus rafinesquei pallescens* Miller, the western big-eared bat; *Eptesicus fuscus pallidus* Young, the big brown bat; and *Antrozous bunkeri* Hibbard, the Bunker pallid bat.

Myotis velifer is a medium-sized cave bat which weighs from 10 to 12 grams in the summer. It ranges from south-central Kansas westward to southern Utah and southern California and south through Mexico to Guatemala.

Corynorhinus rafinesquei weighs from 9 to 10 grams in the summer. This bat's range extends from southern British Columbia south to southern Mexico and is found in caves over most of the western United States. It extends eastward in a narrow belt to western Virginia.

Eptesicus fuscus is a relatively large bat which weighs from around 17 to 21 grams in the summer. It is found all over North America from northwestern Canada and southern Alaska east to Nova Scotia. Its range includes all of the United States and Mexico and extends south to Panama.

Antrozous bunkeri is a large bat weighing from about 20 to 25 grams in the summer. It seems to be endemic to south-central Kansas and northwestern Oklahoma. A near relative, *Antrozous pallidus*, is found in the west from Baja California to British Columbia and south through Idaho and west Texas into central Mexico.

A large colony of *Tadarida mexicana* (Saussure), the Mexican freetailed bat, was studied, but since these bats are not present in the region in the winter, they will be considered in another paper. A male *Pipistrellus subflavus subflavus* (F. Cuvier) was found in Cavern IX (Fig. 2, IX-H) on October 18, 1952, and a female was found in Cavern I (Fig. 2, I-A) on April 12,

1953. No other bats of this species were found, indicating that perhaps the two captured were migrating individuals. Hibbard (1934) reported finding a single *Myotis lucifugus lucifugus* (LeConte) at Cavern XIV on September 3, 1933, and another from Cavern IX on November 4, 1933. No Myotis of this species were found although many forearm measurements were made on small-appearing *Myotis velifer incautus*.

Where the generic name alone appears in this paper, it refers to the species studied in the region in which the work was carried out. The classification used by Cockrun (1952) has been followed.

THE CAVERNS

The caverns in the region (Fig. 1) vary from small sinkholes to rather extensive underground passageways. They are formed in the Medicine Lodge gypsum of the Blaine formation of Permian age. Geologically speaking, all of the caverns are extremely transitory in nature. The formation of these caverns is through water action on the soluble gypsum. Most of the caverns are at the heads of canyons although some remain where the run-off pattern has changed. The largest of the caverns, Cavern II, is of this nature. Cavern I begins on the top of a hill and continues deep into it. A canyon has not yet formed at the base of the hill.

The openings at each end of a cavern allow for free air circulation and thus climatic fluctuation. A homeostatic environment does not exist in caverns whereas in caves, which have only one opening, homeostatic environmental conditions are more closely approximated. Air circulation within caverns is caused primarily by the Venturi effect. Wind blowing over one of the entrances sucks air out of the cavern which causes air to rush into the other entrances. Extremes of daily climatic fluctuation within the caverns are determined by the strength and direction of the wind and the external climatic conditions. In some instances (for example, at point T in Cavern II, Fig. 2), it has been found that although daily fluctuations of temperature are slight, the relative humidity follows the pattern of that outside of the cavern, which usually goes up at night, as the air becomes cooler, and down in the daytime. In this case, it would appear that the walls and the air in the cavern buffer the temperature but not the humidity. Generally, however, temperature fluctuations occur with humidity fluctuations. Temperature fluctuations are, as a rule, much less in the summer than in the winter. This can be explained on the basis that grass around the entrances and leaves on nearby trees reduce the force of the wind.

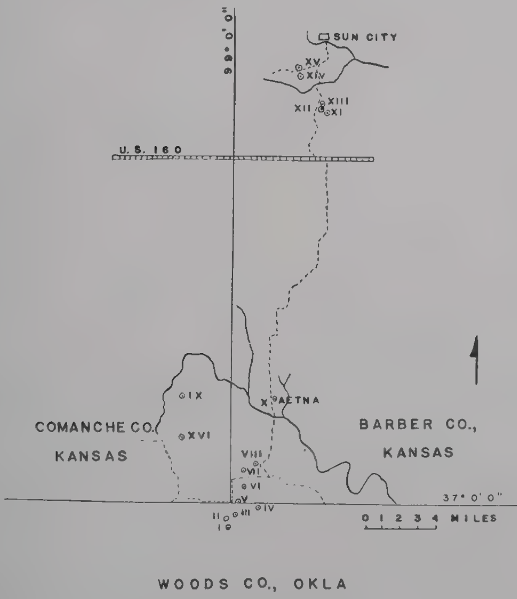

FIG. 1. The geographic location of caverns mentioned in this paper.

All of the caverns in the region differ from one another climatically. These differences are dependent upon the size of the openings and the direction they face, and the length, height and breadth of the cavern. No cavern can be designated as typical either morphologically or climatically. However, it can be stated that all caverns have some daily and seasonal fluctuations of temperature. The center of Cavern IX, for instance (Fig. 2, IX-C), varies from extremes of 0° C. in the winter to 23° C. in the summer (Fig. 8). Daily fluctuation at this point may be as much as 5° C. in the winter, but is rarely more than 1° C. in the summer. Seasonal fluctuations of temperature within a single cavern and differences between caverns are shown in Figures 3, 4, 8 and 11.

Within a single cavern, climatic conditions may differ widely according to the nearness to the entrance, the height of the ceiling, and the amount of air circulation. Dead-end passageways which are by-passed by air currents are generally warmer and more humid than elsewhere in the cavern. Low places are colder than high places. The amount of climatic fluctuation on the ceilings and walls where the bats hang is often dependent upon the degree of roughness of the surface. Very smooth surfaces allow air currents to wash them and thus cause climatic fluctuation. Rough sur-

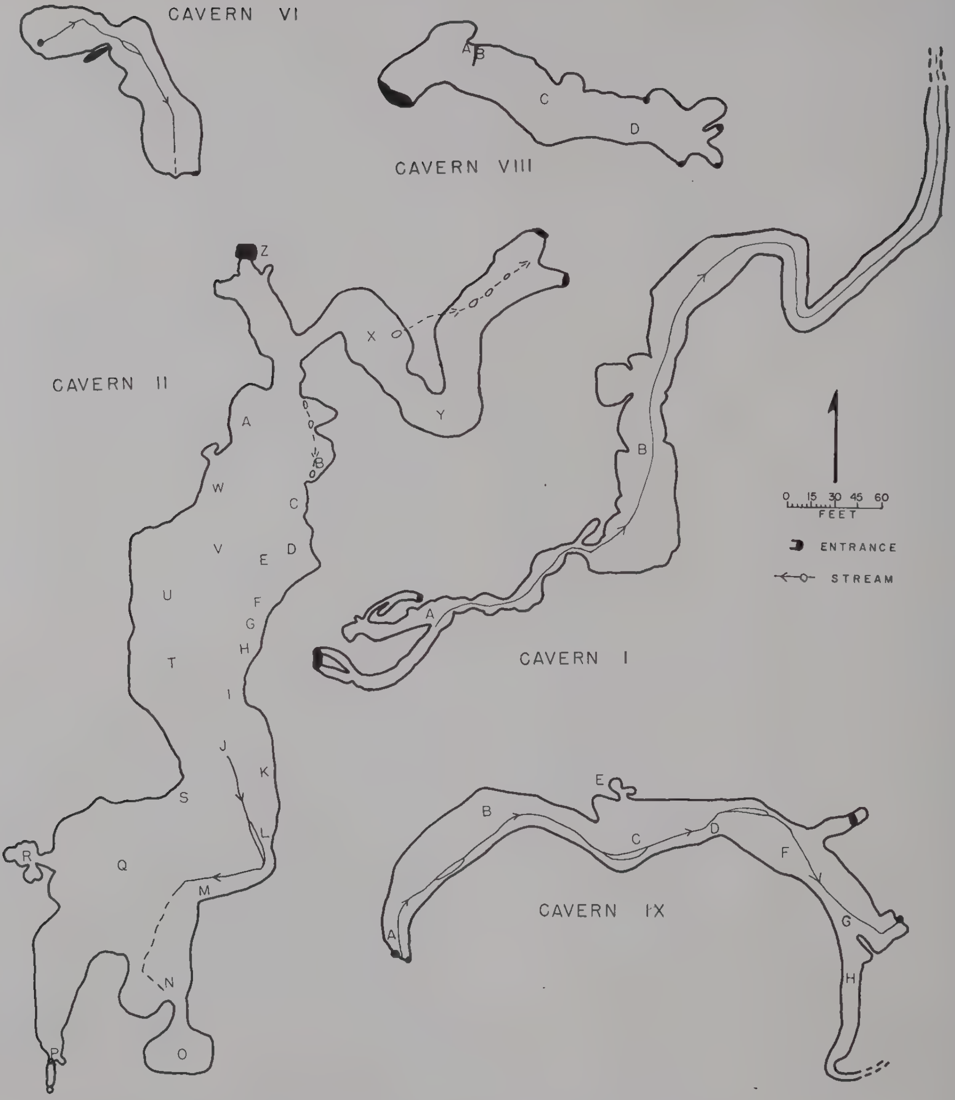

Fig. 2. Diagrams of some of the caverns studied.

faces, on the other hand, break up wind currents which allows for a more constant environment. On rough walls or in undrafty places on smooth walls, the air temperature within one-half inch of the gypsum is usually 1° C. cooler than that of the air two to three inches away. This can be explained by the evaporation of ground water which seeps to the surface of the cavern walls and ceilings.

These caverns offer varied habitat for cavern-dwelling bats in regard to morphological characteristics of the walls and ceilings and climatic characteristics such as temperature, humidity, and the amount of draft. Differences between caverns and within a single cavern would seem to make a study of environmental habitat selection by cavern bats a rewarding one.

It seems best to refer to the caverns by Roman numeral rather than by name. Other localities which are not caverns are also indicated by numerals. The relative location of the caverns is shown in Figure 1. Diagrams of some of the

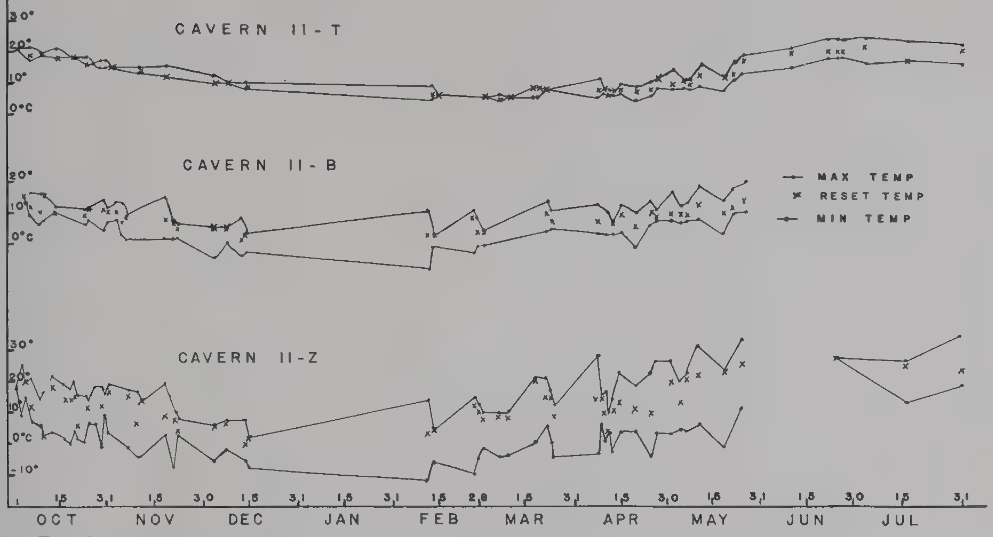

FIG. 3. Maximum-minimum temperature readings at two places in Cavern II. II-Z shows the temperature fluctuation just inside the large entrance.

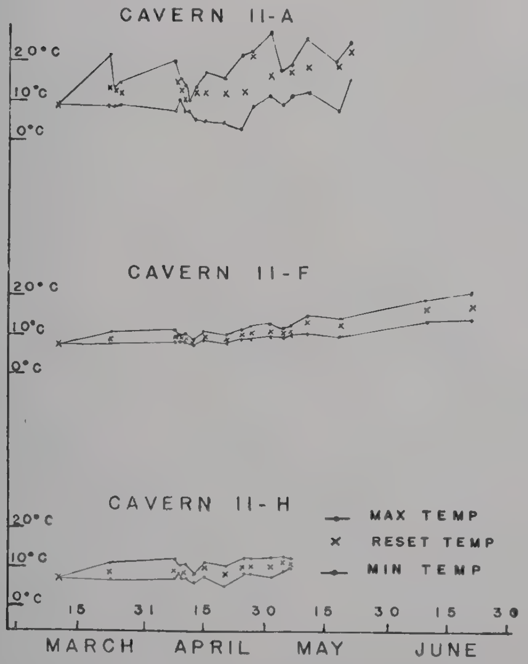

FIG. 4. Maximum-minimum temperature readings in Cavern II. II-F represents a thermometer screwed into a rough ceiling near a thermometer at II-H which was screwed into a smooth ceiling. This shows the effect of wind currents on temperature fluctuation on smooth and rough ceilings.

caverns are shown in Figure 2. The caverns and a brief description of each are as follows:

Cavern I. Unnamed. This is an extensive, low, smooth tunnel with more characteristics of a cave than a cavern as the yearly extremes of temperature extend from a maximum of 18° C. in the summer to a minimum of 14° C. in the winter as determined by a maximum-minimum thermometer set deep within this cavern (Fig. 2, I-B). Relative humidity is always near saturation. A small stream runs throughout its length. This cavern seems to be too warm for bats in the winter and too cool for them in the summer. Small numbers of Myotis are present in the fall. An occasional Corynorhinus is found near the entrance throughout the winter.

Cavern II. Merrihew Cave. This is the largest of the caverns in the region studied. It is probably the oldest as wind and water erosion have caused the gypsum on the walls to expand in large, rough flakes. Most of this cavern, apparently, was formerly continuous although at the present time much of the center is caved in. Generally, the space in the center of the cavern between the letters shown in Figure 2, II represents this fallen rock. Climatic differences and daily fluctuations in different parts of this cavern are great. Two small streams are present. A large population of Tadarida roosts in this cavern from early April until the end of October. In the fall, winter and spring, small numbers of Corynorhinus, Myotis, and Eptesicus are present. A single

Antrozous was captured in the cavern on October 13, 1952. Corynorhinus are the most numerous bats in this cavern, besides Tadarida, in the summer although some Myotis and Eptesicus are also present.

Cavern VII. Lost Colony Cave. This cavern with rough walls and ceilings was named by Laura McMoran in 1953. It is approximately 50 yards in length and consists of five continuous rooms. A small amount of water is present. This cavern harbors a large summer colony of Myotis and in the winter some hibernating Corynorhinus and an occasional Myotis are present. Climatic fluctuations in the summer are slight, but are pronounced in the winter.

Cavern VIII. May's Cave. This is a short cavern with a large entrance and high ceilings. It has rough walls and a dry floor. A hibernating population of Antrozous is in this cavern throughout the winter and large numbers of Myotis are present in the spring. Occasional Corynorhinus and Eptesicus are found here throughout the fall, winter and spring.

Cavern IX. Double Entrance "S" Cave (Hibbard 1934), McMoran Cave of Cockrum (1952). This is a relatively long, low cavern with a stream running through it. A large wintering population of Myotis and a very few Corynorhinus and Eptesicus hibernate in this cavern. Some Myotis are here in July and August although absent in June. An occasional Eptesicus is found in this cavern in the summer. Daily climatic fluctuations are greater in the winter than in the summer.

Locality X. This is an unused barn in Aetna, Kansas, which supports a population of Antrozous and a few Myotis and Eptesicus in the summer. In the fall, numbers of Tadarida are present.

Cavern XIV. Havard Cave. This is a large, smooth-walled cavern with very small entrances. A stream is present. The cavern supports small winter and summer populations of Corynorhinus and Myotis. Large accumulations of guano attest that huge numbers of feeding Myotis previously utilized this cavern in the summer. Summer and winter daily climatic fluctuations are slight. This cavern now seems to be too cool for Myotis in the summer. Small entrances resulting from cave-ins would make this cavern assume the morphological characteristics of a cave and would cause it to be cooler in the summer than if a large entrance were present. This might account for the fact that it is no longer used by a large population of feeding Myotis.

Locality XV. This is a smooth, wet, unused mine shaft of a gypsum mine still in operation. It contains a number of Myotis in the fall and winter along with a few Corynorhinus and Eptesicus. No bats were found here in the spring and it was not studied in the summer.

Materials and Methods

Caverns were explored to determine the location of bats. An eight cell headlamp furnished light and when observations were being made on active bats, the lens was often shielded with three or four layers of red cellophane. Disturbance of the bats was avoided as much as possible. Many Myotis and all of the Corynorhinus, Antrozous and Eptesicus caught during the fall, winter and spring were loosely banded on the right forearm with U. S. Fish and Wildlife size 0 bird bands. Banded bats were usually released a short distance away from the cavern in which they were captured although Antrozous were replaced in the crack from which they were taken.

Ambient (micro-environmental) and rectal temperatures were taken with Schultheis reptile thermometers accurate to 0.2° C. Ambient temperatures were determined by hanging the thermometer one-half inch away from the wall or ceiling where the bats were found and leaving it for a minute. The thermometer was read from a distance of three feet using the edge of the beam of light so that heat from the body of the observer and the headlamp would not influence the readings. Taylor maximum-minimum thermometers accurate to 0.5° C. were either screwed into the gypsum ceilings of the caverns or else stuck in cracks. All maximum-minimum graphs in this paper with the exception of II-B (Fig. 3) and VIII-A (Fig. 11) reflect temperature changes within one-half inch of the rock.

Until the end of February, 1953, relative humidity figures were obtained by means of a small sling psychrometer slung as close to the rock as possible. After the beginning of March, a Bendix-Friez aspiration psychrometer was utilized, the thermometers being held within one-half inch of the rock. Continuous temperature and relative humidity data were obtained with Bristol model 4069th recording thermohumidigraphs. The accuracy of these instruments was checked weekly with the aspiration psychrometer.

Light readings were taken with a Weston Master II exposure meter; the measurements were obtained by pointing the light receiving unit of the instrument straight up.

Bats were weighed by tying them in small cheesecloth sacks and placing them on an Ohaus double-beam balance accurate to 0.1 gram.

Rough diagrams of some of the caverns (Fig. 2) were made by compass and placing.

In the course of this study about 1800 Myotis, 200 Corynorhinus, 70 Eptesicus and 30 Antrozous were handled. Many other Myotis, Antrozous and Corynorhinus were observed in summer quarters. No summer concentrations of Eptesicus were found.

This study began on September 13, 1952. Except for a period from December 18, 1952, to February 8, 1953, it was continuous until August 8, 1953. Two weeks were spent studying the caverns in the last half of December, 1953. When in the field, an estimated average of two to three hours a day were spent inside the caverns.

WINTER BEHAVIOR AND HABITAT SELECTION

Hibernation

The problem confronting hibernating bats is the maintenance throughout the winter of a low enough metabolism so that the fat reserves are not used up before the end of the hibernating season. Burbank and Young (1934) and Swanson and Evans (1936) suggested that food from within the caves such as spiders and crickets is taken throughout the winter to supplement fat storage. Hahn (1908), Folk (1940), and others maintained that hibernating bats live wholly on bodily food reserves. No evidence has been observed of winter feeding in any of the species here studied. Four Antrozous from Cavern VIII and ten Myotis captured at Cavern IX on December 31, 1953, were kept in captivity in cold rooms and were given only water and no food. The Myotis lived until the middle of March, 1953, and three of the Antrozous were still alive at the end of April, 1953. Feces were occasionally dropped during this period.

Irritability and the Function of the Cluster. Hahn (1908), Swanson and Evans (1936), and Folk (1940) stated that various degrees of torpidity are evident in hibernating bats. By this, they meant that some bats would awaken from hibernation more readily than others. This phenomenon was noted quite regularly in this study. Rather than the degree of torpidity, however, it is perhaps better to speak of the degree of irritability, since the body temperature of bats difficult to awaken and bats easy to awaken may be the same.

It is postulated that the amount of disturbance required to awaken a torpid bat is dependent upon how high or how low the body temperature has been during a given length of time that the bat has been in a torpid state. In other words, the degree of irritability of a hibernating animal is directly related to the area under the time-temperature curve.

It has been found that once the awakening reaction is initiated in a torpid bat, the process of a constant and rapid temperature rise (about 0.6° C. per minute for Corynorhinus, 1.0° C. for Eptesicus, and 1.1° C. for Myotis) continues until the bat reaches a body temperature at which it is capable of flight. This has been found to be a rectal temperature of 24° C. for Corynorhinus, and around 30° C. for Myotis, Eptesicus, and Antrozous. Corynorhinus does not fly agilely, however, until a rectal temperature of 28° to 30° is reached.

Observational and temperature data indicate that bats remain hanging longer where there is a constant low temperature with little breeze than at places with fluctuating low temperatures or constant high temperatures. Bats hibernating in warm places are usually more irritable than those which have been hibernating in colder ones.

The awakening reaction of some of the members in a cluster of Myotis can be triggered by shining a light on the cluster. Others in the cluster, the majority, will remain torpid unless a more violent disturbance is made. Proportionately, it has been found, the greater numbers of irritable bats tend to be on the edges of the clusters. This was observed many times by means of shining a light on a cluster and holding it there until many of the bats were awakened. Clusters form from the center outward, the bats being so closely packed together that it is impossible for a flying bat to become a member of the cluster anywhere but on the edges. Consequently, those on the edges must necessarily have been members of the cluster a shorter period than those in the center considering that the build-up of a cluster is a gradual thing.

The irritability of the peripheral bats apparently can be attributed to the higher temperature at the edges of the cluster. This implies a higher body temperature and thus a higher metabolism of those bats at the periphery. Many temperatures were taken throughout the study within the clusters and at the edges by means of a Schultheis reptile thermometer. The bats in these clusters are so closely packed that they support the weight of the thermometer when it is placed among them. Temperatures at the edges of the clusters were generally from 0.2° C. to 1.0° C. higher than those inside the clusters. Rectal temperatures of bats taken from within and at the edges of the clusters show the same gradation. Temperatures taken against the gypsum rock tend to be the same as the rectal temperatures of the bats in the interior of the cluster whereas the temperatures of the bats at the edges are somewhat higher than the rock temperature. The temperature of the air one inch below the gypsum is about 1.0° C. higher than the rock whereas that of the air six inches to one foot away is two to three degrees higher. The rectal temperature of a bat hanging singly is usually about 1.0° C. higher than the temperature of the gypsum.

Further evidence indicating that the degrees of torpidity are actually degrees of irritability was found when working in Cavern IX. After two weeks of no known disturbance, a number of torpid Myotis are easily awakened and these always fly. On the following day, however, it has been found that all of the bats in the cavern are equally difficult to awaken, none showing irritable characteristics.

Hock (1951) showed in a summary of the literature that the body temperatures of bats approximate the temperatures of the micro-environment in which they are resting. Numerous rectal temperatures taken throughout this study substantiate these findings. A bat hibernating in a dense cluster, all members of which are losing the heat of metabolism to a nearby rock surface, is little affected by warmer air circulating beneath it. This bat will, in consequence, have a lower body temperature and thus a lower metabolic rate allowing it to be better situated for a long period of hibernation than a bat hibernating in a more exposed, and thus warmer situation.

The function of clustering during hibernation, therefore, would appear to be not the conservation of heat as supposed by many authors, but rather a protection from heat. A bat closely packed in a cluster with only the head and wrists projecting is not washed and warmed by the circulating air. Instead, a bat protected by the bodies of other bats can lose metabolic heat quite readily to the gypsum which has a much higher heat conductivity than either air or water. Consequently, the metabolic rate of a bat with a low body temperature, the same as that of the rock, would be minimal.

A Proposed Reason for Irritability. Since the bats that are more exposed to the environment of the outside air due to air circulation are more irritable than those in clusters or in cracks, the factor causing irritabilty and thus awakening may be the amount of stored food that has been catabolized. The primary wastes of metabolism are carbon dioxide, nitrogenous byproducts and water. The observation that Myotis when awakened nearly always urinated in a behavior pattern to be described later suggests that a possible factor causing awakening is the amount of urine in the bladder and the nervous consequences of an extended bladder. This would explain the degrees of irritability and would be a direct link to the environmental temperature and the rate of body metabolism.

Guthrie (1933) suggested that thirst may be a factor causing awakening. Thirst is a secondary result of metabolism, but it is here believed that the direct factor causing awakening is the stimulating effect of an extended bladder on the nervous system. Johnson (1931) reported that hibernating ground squirrels always awoke with full bladders and rectums and that they always voided after becoming active.

The higher metabolic rate at temperatures approaching freezing as shown by Hock (1951) would have the same effect on the amount of food catabolized as higher temperatures. Adler (1926) found that as 0° C. was approached bats tended to awaken naturally. Other workers (Allen, 1939) indicated that bats die when in temperatures lower than freezing. This is not substantiated by field observations in this study as no bats were found dead during the winter although they had been hibernating in places which registered 0° C. or below according to maximum-minimum thermometers placed nearby. These bats had always moved after freezing temperatures.

Climatic Habitat Selection

Each species of bat in this study has a type of habitat selection which is effective but which to a degree seems to be a trial-and-error system. If the place that a bat selects for hibernation is unsuitable, the bat after a period of time awakens, probably because a high metabolic activity has made it irritable. The behavior of all of the bats except Antrozous is to move to a new place within the same cavern or to another cavern. If the next place chosen is unfavorable, the process is repeated until a more favorable site is found and the length of time in torpor is greater due to decreased metabolic activity. The social tendency of the bats here studied to seek their own species increased the probability of most of the individuals finding places that remain suitable longest.

Temperature. Climatic selection of habitat for hibernation is made by Corynorhinus, Myotis, and Eptesicus to the extent that the relatively cooler parts of the caverns are utilized. Data gathered in this study indicate that the sense of temperature selection for bats seeking a place to go into hibernation is not especially good. Apparently, they can discern rather wide variations in temperature as the warmest parts of the caverns are never

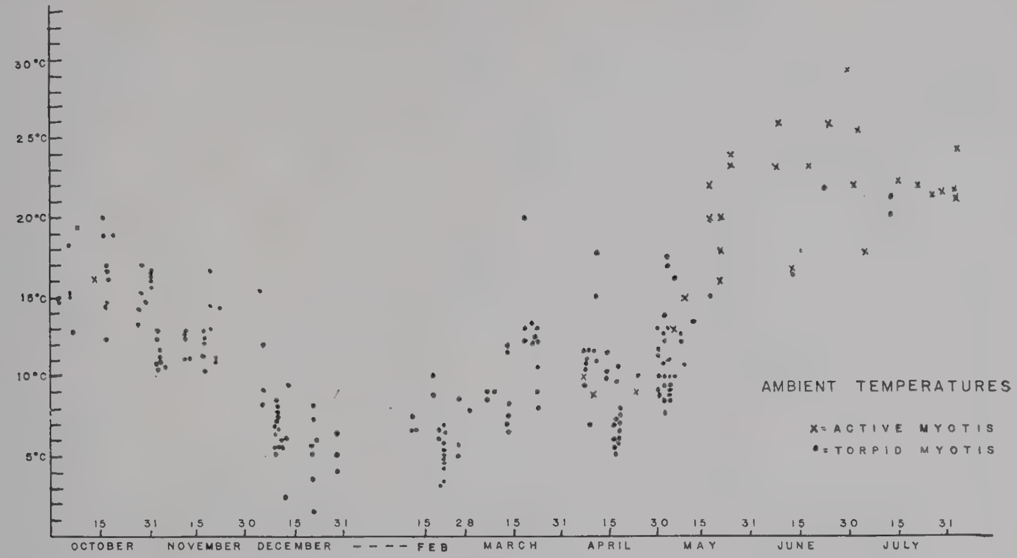

FIG. 5. Micro-environmental temperatures at which *Myotis velifer* were found. Many caverns are represented.

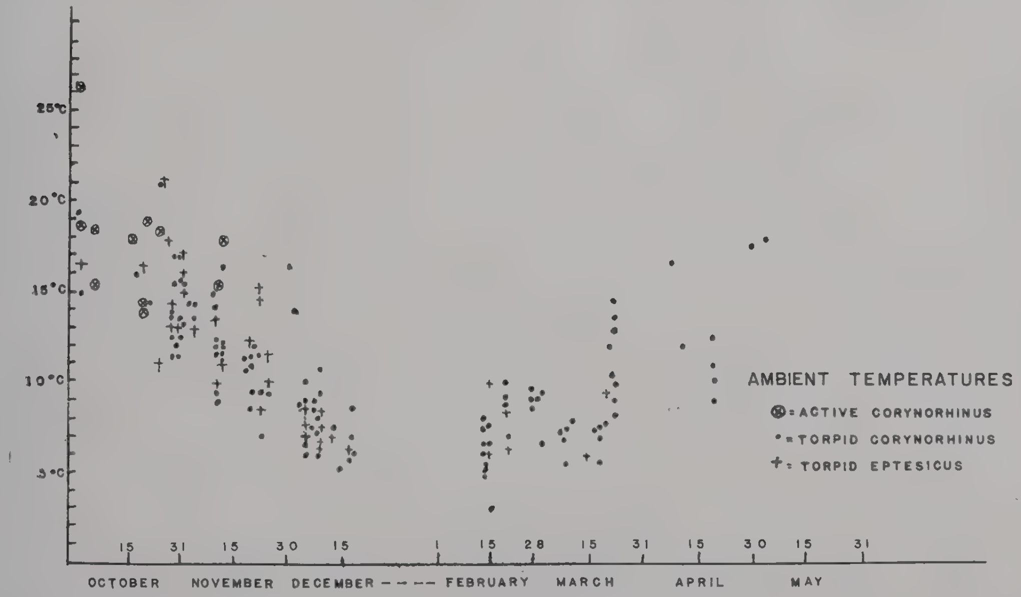

FIG. 6. Micro-environmental temperatures at which *Corynorhinus* and *Eptesicus* were found. All caverns are represented.

utilized for hibernation. For example, at point T in Cavern II (Fig. 2, II-T) the winter temperatures are always somewhat higher than in the rest of the cavern (Fig. 3 and 4), and although the topography of the cavern is suitable and the humidity as high as in the other caverns, bats have never been found at point T in the winter. Bats are frequently found at cooler places nearby. Ambient temperatures taken one-half inch from the wall or ceiling at the exact point where bats were found vary quite widely on a given day even within a single cavern (Fig. 5 and 6). These temperature graphs for Corynorhinus, Myotis, and Eptesicus superimpose perfectly, showing no gross species temperature preference.

Relative Humidity. The idea that high relative humidity is an essential factor for bat survival has been often stressed. The results of this study do not indicate that this is necessarily true for these bat populations (Fig. 7). The relative humidities vary greatly from cavern to cavern and from day to day within the caverns. The relative humidities of all of the caverns are greater than those outside at all seasons of the year. Parts of the caverns that have the highest relative humidities are, in fact, never occupied by torpid bats. This can be attributed to the observation that these are the warmer places which bats going into lethargy in the winter seem to avoid. These warm localities within the caverns are always relatively high places where there is little air circulation and warm air is trapped. Such a place is in Cavern IX (Fig. 2, IX-E).

The importance of relative humidity is, apparently, somewhat different for different species of bats. A *Myotis l. lucifugus* caught in the fall and left overnight in a heated building in Ann Arbor, Michigan, was found to have dried wing membranes the next morning although the bat was still alive. A *Myotis velifer incautus* from south-central Kansas was placed in a similar building in Ann Arbor for three days in February and at the end of that time there was no desiccation of the wing membranes. *Eptesicus f. fuscus* from Ann Arbor do not desiccate in similar situations.

Light. Most Myotis do not hang in places that are even dimly lighted when selecting a place for hibernation. Hibernating Corynorhinus, on the other hand, are found in places which vary from broad daylight to total darkness. Eptesicus and Antrozous are often found in dimly lighted places.

Habitat Selection of Myotis

Hibernating Myotis were found in nearly all of the caverns studied, but concentrations of over several hundred individuals were constantly present only in Cavern IX. These bats tend to form clusters of varying sizes on relatively smooth ceilings. As mentioned previously, the cooler parts of the caverns are utilized for hibernation and drafty places generally avoided.

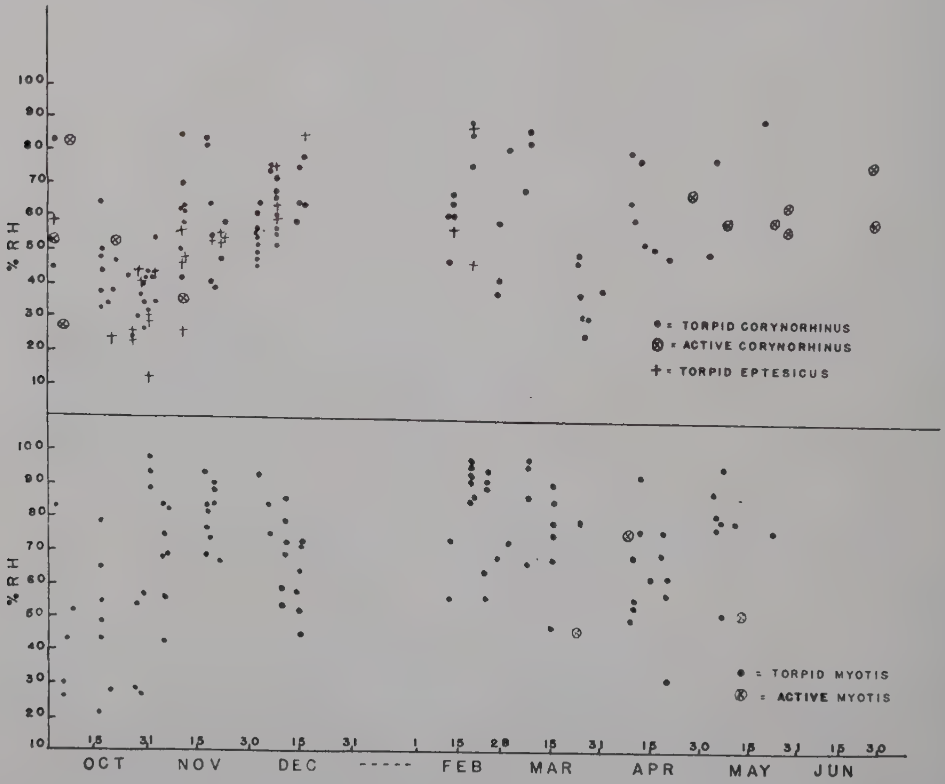

FIG. 7. Relative humidities where *Corynorhinus, Eptesicus,* and *Myotis* were found. All caverns are represented.

When single Myotis are found in drafty situations, however, they hang by the thumbs as well as the hind feet. This brings the ventral part of the body close to the rock thus avoiding some of the circulating warm air. When hanging singly in undrafty situations, the usual head-downward posture is assumed. In drafty situations, Myotis often hibernate in crevices, but these are not preferentially utilized since there are always empty crevices in the caverns which had contained bats on previous visits. Stager (1939) stated that *Myotis v. velifer* was decidedly a "crevice dweller." This is not true for this population of *Myotis velifer incautus* in either summer or winter, as crevices are only occasionally occupied.

The height that Myotis hang in Cavern IX seems to be determined partly by temperature and wind currents. There are smooth ceilings about 10 feet high from IX-A (Fig. 2, IX) to just before IX-C. There are sometimes a few Myotis hibernating on these ceilings, but the great majority in this part of the cavern are hanging four to five feet from the floor on a rougher, low ceiling a few feet to the south. Higher temperatures and greater air currents seem to make the high ceiling unfavorable. The minimum height that Myotis hang in this cavern seems to be partly determined by greater air currents in the low places where suitable ceilings are present. This is illustrated by the maximum-minimum thermometer set at IX-D (Fig. 8, IX-D) which shows that temperature fluctuation here is greater than elsewhere in the cavern. The thermometer was screwed into the ceiling two and one-half feet above the floor. This is the place of smallest diameter in the cavern and air currents are fastest at this point.

Movement of clusters. The effect of environmental fluctuation upon habitat selection is illustrated by Figure 9 showing the distribution of clusters of Myotis in Cavern IX at various times during the hibernating season. In the fall and

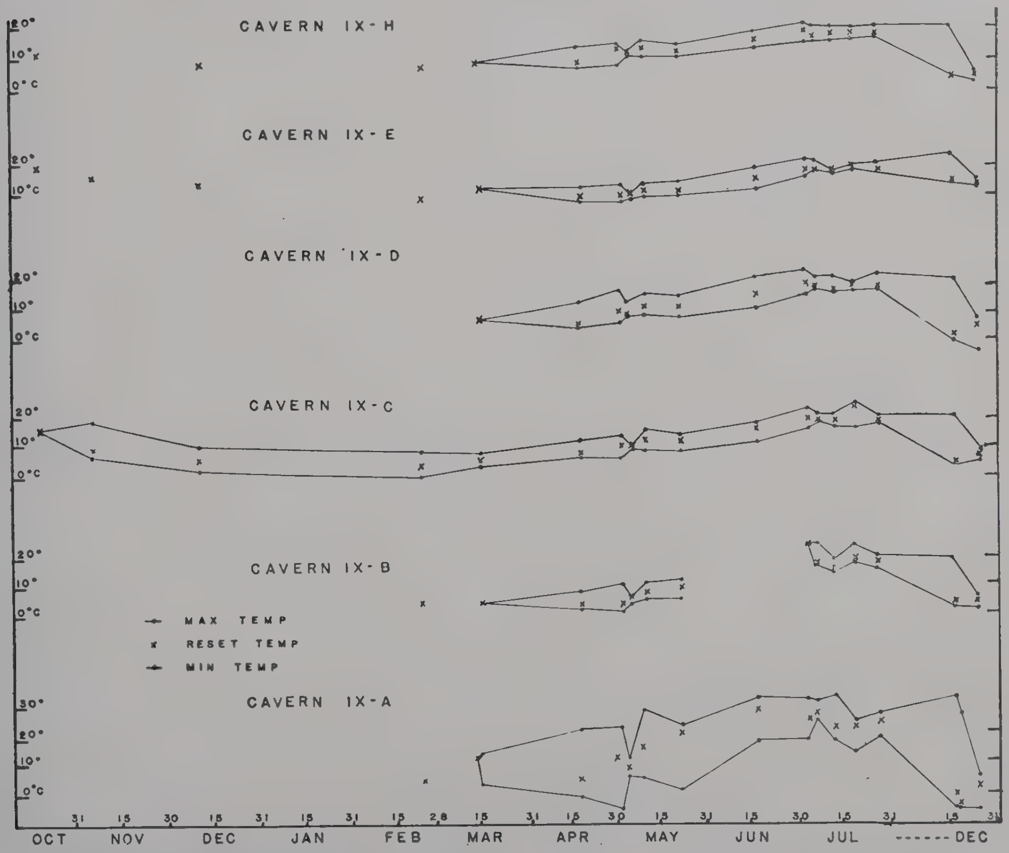

FIG. 8. Maximum-minimum temperatures at different parts of Cavern IX. IX-A shows temperature fluctuations just inside the entrance.

spring, the bats are distributed throughout the cavern in relatively small clusters. Many singles and doubles are present during these times. As the hibernating season progresses, the numbers of singles and doubles decrease, the size of the clusters increases, and the majority of the bats seem to have found the most favorable parts of the cavern.

The estimated numbers of Myotis in Cavern IX fluctuated throughout the winter. These estimates are as follows: December 11, 1952, 4,243; February 24, 1953, 4,655; March 15, 1953, 6,095; April 18, 1953, 3,558; May 2, 1953, 178; and December 23, 1953, 7,331. These estimates were obtained by measuring and counting clusters and individuals in the cavern. Twelve clusters of various sizes were measured as squares or rectangles and the area calculated. The bats were then counted and the mean result for these 12 clusters was 1.1 Myotis per square inch.

The hypothesis suggested by these movement data is that those Myotis in the colder, less fluctuating parts of the cavern metabolize at a slower rate, move less often, and thus make a nucleus for active bats to hang up rather than at the more unfavorable places. The movement of a number of clusters, for instance those from IX-H (Fig. 9, December 11, 1952) and elsewhere in the cavern, can be explained on the basis that those bats in the less favorable places will catabolize more stored food and thus awaken sooner than bats in more favorable situations. Figure 8 shows that maximum and minimum temperatures at IX-H and IX-C are about the same. However, recording thermohumidigraphs set at the same time and at equal distances from the ceiling at IX-H and IX-C (Fig. 10) show that at IX-H the climate fluctuates much more. This indicates that this part of the cavern is more windy and the layer of cold air next to the gypsum is much less stable than at IX-C where the fluctuation is slight. The bats, particularly those on the periphery of the clusters at IX-H, then, would be washed with warm air more than those at IX-C and would, in consequence, catabolize at a higher rate.

As stated previously, bats on the periphery of clusters are more irritable; as they awaken they move, thus exposing the next layer of bats in the

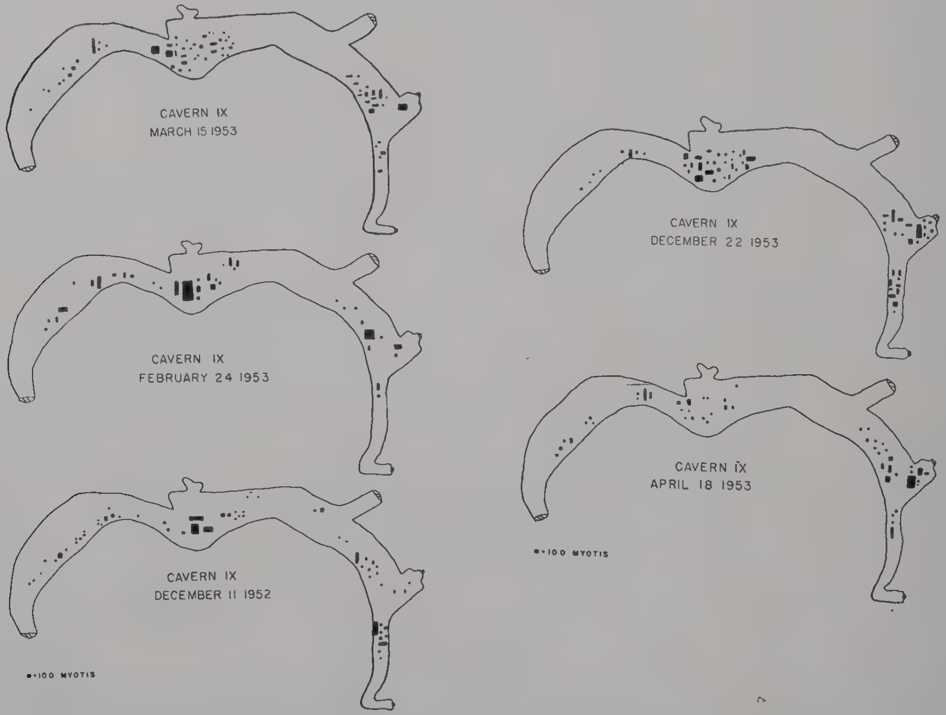

FIG. 9. The distribution of clusters of *Myotis velifer* in Cavern IX at different times during the hibernating season.

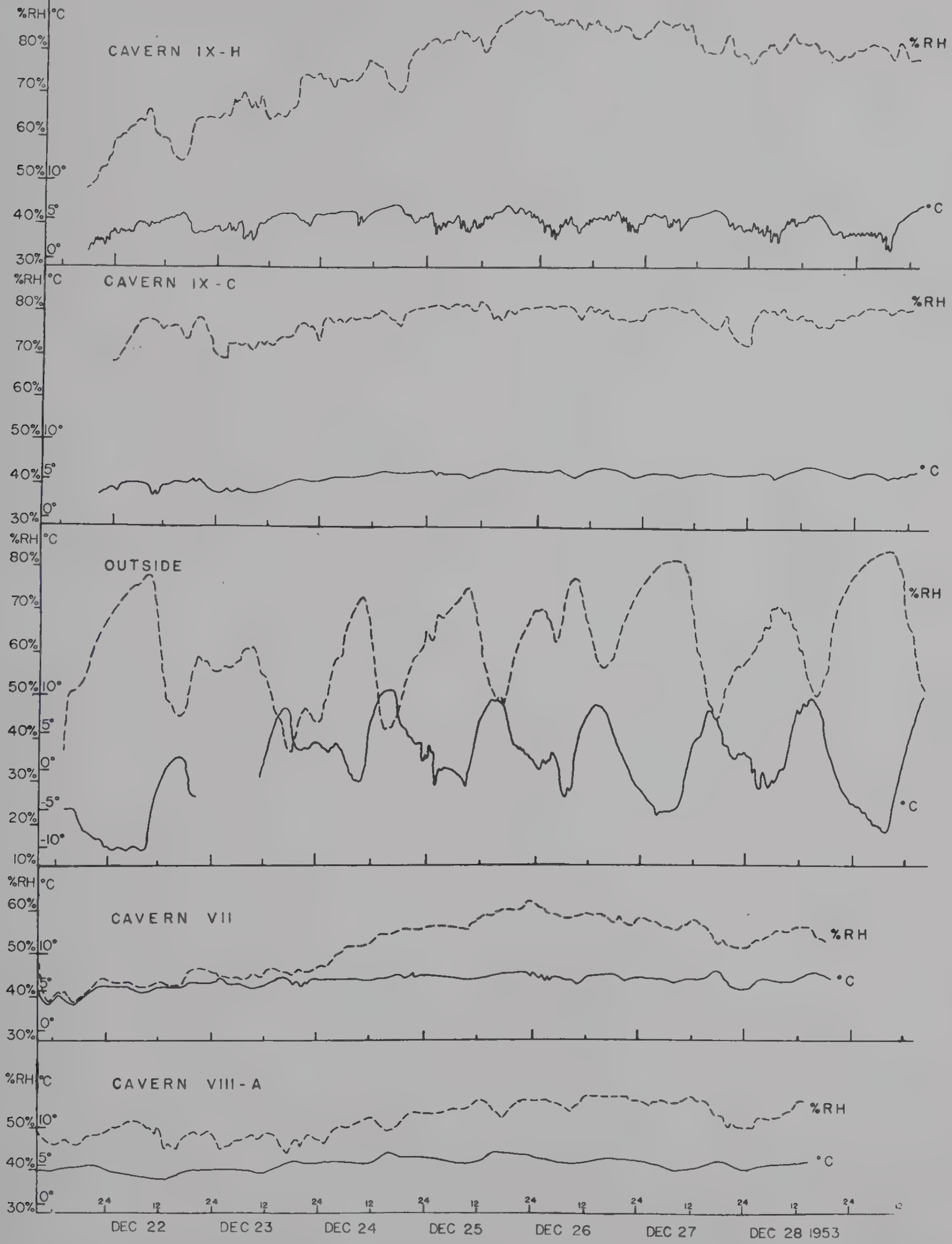

FIG. 10. The effect of the external climate on the climate of some caverns. These are thermohumidigraph records from different places taken at the same time. "Outside" is a record obtained by hanging the instrument five feet above the ground in a protected place on the north side of a house near Locality XVI (Fig. 1.)

clusters to the warmer environment. Those in the center of the cluster, of course, also eventually move since they, too, were at one time exposed at the periphery of the cluster during its formation. In addition, the result of even a very low rate of metabolism will force them to awaken and move at a maximum time of around a month.

The shift of clusters from place to place during the hibernating season would seem to be the direct result of environmental temperatures on the metabolism of those bats within, but particularly on the periphery of the clusters. The tendency of the Myotis to hang in the colder parts of the caverns, their instinct to form clusters, and their avoidance of drafty places at the time they hang up increases the probability that a suitable place is selected. A shift in outside wind direction after they are torpid may make the place selected unfavorable in a short period of time. Many bats in such a system would be in the more unfavorable parts of the cavern at any period of the winter, but the proportionate number will gradually be decreased as those in the coldest, least fluctuating part of the cavern during the winter months will remain asleep longest. As warmer weather begins, bats in all parts of the cavern will metabolize at a higher rate and cluster breakup will be evident even at the most favorable places. This appears to explain the spread-out distribution of bats throughout the cavern in the fall and spring. Disturbance may have speeded up this process of movement, but it is not believed that the basic pattern was altered since only a small part of the population was disturbed at each visit, and the cavern was infrequently studied in an effort to avoid disturbance of the hibernating bats.

The results from this study indicate that the shift of bat populations described by Guthrie (1933) and Folk (1940) were the result of the same sort of habitat selection which is, within a cavern, more random than might be expected.

Behavior upon awakening. Hahn (1908) found that the bats he studied in Indiana were more active and easily awakened during the latter part of the winter than in the fall and early winter. The opposite was found in this study in that more bats are flying in the caverns in the fall and spring than during the cold weather of winter. Myotis were seen flying in Cavern IX at all times of the day and night during the winter. Apparently, these bats do not conform to any cycle of periodic activity as reported by Griffin and Welsh (1936) for active bats which awakened in the evening though fed at odd intervals. Folk (1940) suggested that this periodicity also applied to hibernating bats.

Since it was impossible not to disturb some of the hibernating Myotis while working in the caverns, the following behavior was noted in Cavern IX on many instances. Upon first entering the cavern, several bats might be flying. After approximately 20 minutes of disturbance several more would be active, and if work continued for several hours hundreds of Myotis would be awakened and flying about the cavern. The noises made by the flying bats tend to awaken other torpid bats. These flying bats would soon congregate at IX-E (Fig. 2, IX-E). The temperature at this place during the winter is always 3° C. to 8° C. warmer than the parts of the cavern where the Myotis hibernate (Fig. 8). This place is a concavity from 18 inches to six inches in diameter and about a foot deep. It is six feet above a dry floor in a very small room. This is very little air circulation here and the relative humidity is higher than at any other place in the cavern. Fifteen minutes after releasing bats banded from a single cluster at the mouth of the cavern, this concavity would contain nearly all of these banded bats. From one to three hours after going to this concavity, the bats redistribute themselves throughout the cavern. On the basis of banded bats released together, it was determined that these bats have no tendency to form a discreet cluster; rather they become scattered indiscriminately among the other clusters throughout the cavern or else are found as singles. When Myotis are disturbed from their lethargy, they are never observed to urinate while flying as they do in their summer quarters. Myotis caught flying into IX-E usually urinate upon being examined and droplets of urine are present on the wall of the concavity after it has been visited by many bats. The concavity itself smells strongly of bat musk. The same type of behavior after awakening has been noted for Myotis in Caverns I, II, XIV, and XV, the disturbed bats in each instance forming loudly squeaking clusters in the warmest parts of the caverns.

Copulation in Myotis was never positively ascertained although bats that appeared to be copulating were observed in the concavity (E) in Cavern IX on many occasions. Wimsatt (1945) observed copulating *Myotis l. lucifugus* after disturbing a hibernating colony. These bats were active. He also attributed copulation to pairs of torpid bats in which he found that the male's penis was erected. This interpretation is considered erroneous, since torpid Myotis, Eptesicus, and Antrozous are often found with erected penes away from other bats. No copulatory behavior was observed in Corynorhinus although this was described by Pearson, Koford, and Pearson

(1952) who found that active males copulated with torpid females. Guilday (1948) apparently found behavior in *Myotis l. lucifugus* in Pennsylvania similar to what is here described for *Myotis velifer incautus.* He stated: "Ahead in the darkness, however, others could be heard squeaking before they were disturbed. After they were disturbed, some took flight immediately, while others, although they remained hanging were breathing heavily. Their fur was wet and muddy. Two pairs of *Myotis lucifugus* were found in active copulation."

That this behavior pattern, found in the Myotis in Cavern IX and elsewhere, is related to reproduction, is further suggested in that the concavity in Cavern IX was used by fewer active bats in March than during the rest of the winter and by the middle of April was not used at all although many torpid bats were awakened. Eisentraut (1950) stated that *Myotis myotis* in Germany breed throughout the winter in hibernating quarters. It seems to have been substantiated by other workers that bats in hibernating quarters breed primarily in the fall and winter and that very few breed in the spring.

Awakened Myotis in Cavern IX in the winter sometimes drink from small pools of water in the cavern by dipping into them when flying. It is not known whether they drink before or after going to the concavity at IX-E.

Habitat Selection of Corynorhinus

The principles of habitat selection relating temperature to metabolism apparently apply to the other species of bats studied in the caverns. A very few small clusters of hibernating Corynorhinus have been seen, but most of these bats have been found singly on walls although often with other Corynorhinus nearby. These bats are sometimes near the entrances of caverns in lighted places and nearly always on very rough walls. As evidenced by temperature readings, temperature fluctuations are greater on smooth than on rough surfaces. This is illustrated by Figure 4, II-F and II-H. The maximum-minimum thermometer at II-F was screwed onto a rough ceiling four and one-half feet above floor level at the same height as II-H which was screwed onto a smooth ceiling deeper into the cavern. Wind currents, the cause of temperature fluctuation, nearly always travel from II-F towards II-H so that air coming into the cavern would reach the thermometer at II-F first. These graphs show the apparent advantage of selecting rough places in the cavern for hibernation. During the winter, many Corynorhinus were found in places where wind currents and consequently temperature fluctuations are great, but the length of time that these bats remain torpid is much shorter than for those which hang in more favorable places. Even in these situations, Corynorhinus usually hang in slight concavities or behind bumps on the rough walls. Air currents are slight in these places despite strong breezes few inches away. This was determined by the flow of cigarette smoke. Figure 10, VII is a thermohumidigraph record where the instrument was placed very near a torpid Corynorhinus in Cavern VII. This bat remained at the same place during the time that the instrument was operating.

The hibernating position of Corynorhinus is somewhat different from that of other bats. The long ears are folded along the sides of the neck and the fingers of the wings are unfolded, meeting at the midline of the belly; the tail membrane is folded against the wings. This hibernating posture provides an insulating pocket of dead air all along the ventral side of the bat. This would act as insulation against warm air. The lack of circulation to the wings during hibernation due to the action of vasoconstrictors in the wings of bats noted by many authors allows the wings to change temperature without greatly influencing the body temperature. The relatively long fur on the back, which stands perpendicular to the body during hibernation, gives further insulation against the surrounding warm air. This position of hibernation and the long fur would seem to insulate the torpid bat not so much against the cold, but particularly against the warmer air, the metabolic heat being lost to the gypsum and the bat assuming the temperature of the gypsum.

Habitat Selection of Eptesicus

Eptesicus usually hibernate singly in small, horizontal crevices on the ceilings of caverns. The fact that Eptesicus were often found near the entrances and avoided the more humid and warmer parts in the caverns as noted by Rysgaard (1942) does not imply that they are particularly hardy bats, but rather they have ability to select cool hibernation habitat that is most often well suited to their metabolic needs. Writing about *Eptesicus f. fuscus* in Ontario, Hitchcock (1949) stated: "Although in the draftier locations I have usually found them somewhat sheltered in cracks, they seem to prefer a spot where there is air movement." The presence of air movement below the cracks, however, does not mean that the bats themselves are exposed to these currents. The evaporation of water from the usually damp gypsum would tend to make the rocks cooler, and for an animal hibernating in a position where both the ventral and dorsal surface of the body touches the rock, this would appear to be of metabolic advantage. In these crevices, the flow of air, as measured by cigarette smoke even in the draftiest locations where these bats are found, bypasses the torpid Eptesicus. A maximum-minimum thermometer was hung four inches from the ceiling (Fig. 4, II-B) directly below a horizontal crack where Eptesicus are found, from time to time, throughout the winter; this shows the temperature fluctuation at this place, and illustrates that the air currents flowing by bring air from the outside. Hitchcock (1949) went on to say that perhaps the degree of dryness was a factor in selecting proper habitat rather than draftiness. No evidence of this was found in the race (*pallidus*) observed in this study (Fig. 6) except that the colder places in the caverns that the bats select are usually drier than the warmer places.

Habitat Selection of Antrozous

Antrozous were found during the hibernating season in only one place—a crack in the ceiling of Cavern VIII (Fig. 2, VIII-B) 54 feet from the large entrance and 10 feet above the dry cavern floor. This crack extends more than seven feet into the ceiling of the cavern and varies from one and one-half inches to three inches wide at ceiling level to one inch wide near the top. A hibernating colony of approximately 20 individuals was present throughout the winter of 1952; in December, 1953, over 100 individuals were counted. Both sexes were present. These downward-hanging bats always face the same direction, their bellies against the south wall of the crack with their long ears extended. Disturbance did not cause them to move to another part of the cavern or to another cavern as it did the other bats in this study, but rather they crawled higher into the crack. If not disturbed for a week or so, they would again be from four inches to two feet above the ceiling level of the cavern. The tragi of seven old males showed indications of having been frozen since the tips were withered. This indicates that either in the fall or spring the bats were in other, more unfavorable places as maximum-minimum temperature readings six inches in the crack (Fig. 11, VIII-B) do not indicate that freezing temperatures are ever reached in this crack despite its nearness to the large entrance and the free flow of air throughout the cavern. The maximum-minimum thermometer hanging two inches below the crack (Fig. 11, VIII-A) shows the protection given by the crack by moderating temperature fluctuation. A thermohumidigraph hung directly below the crack during a very cold period (Fig. 10, VIII-A) shows the climatic fluctuation at ceiling level. These measurements indicate that Antrozous hibernate at warmer temperatures than the other species in this study. This is not surprising since Antrozous is a relatively large bat and does not have the metabolic problems of a bat half its size.

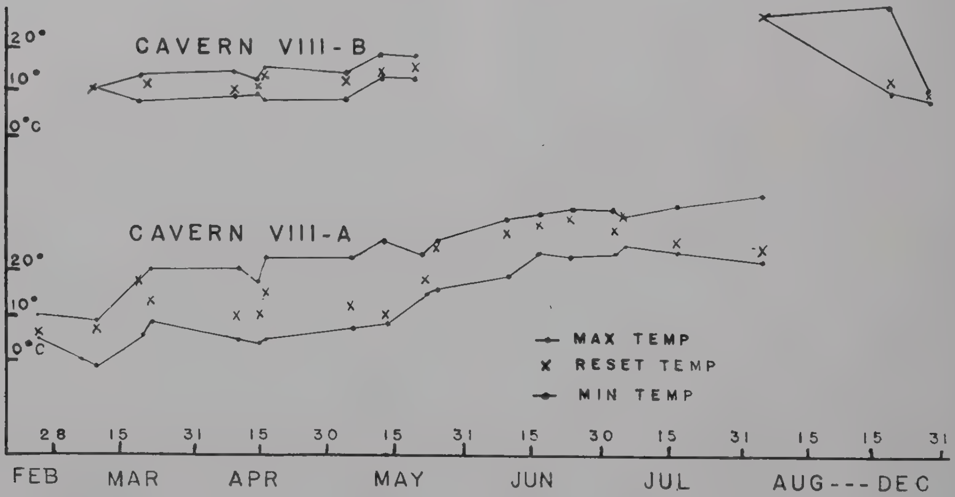

FIG. 11. VIII-B shows maximum-minimum temperatures six inches within the crack where *Antrozous* hibernated. VIII-A shows maximum-minimum temperatures four inches below the ceiling level just beneath the crack.

Relative humidity readings taken six inches within the crack varied from 17 per cent to 92 per cent in March and April, 1952. This figure is on the average 10 per cent higher than at the ceiling level below the crack. On December 21, 1953, the relative humidity in the crack was 68 per cent and that below the crack was 77 per cent. Two Myotis were found hibernating with the Antrozous, one in December, 1952, and the other in March, 1953. The narrower part of this crack which the Antrozous do not use was filled with Myotis in April and May, 1953. The Antrozous were last seen in the crack on March 23, 1953. An active male Antrozous was found at point Y in Cavern II (Fig. 2) behind a flake of gypsum on the rough wall on October 13, 1952.

Hibernating *Antrozous bunkeri* have not been found anywhere but at Cavern VIII. The fact that this is the first sizable colony of hibernating Antrozous that has been reported is probably due to their habit of hibernating often out of sight in deep, narrow cracks. Orr (1954) reported five instances where four or fewer *Antrozous pallidus* were found hibernating. He has successfully kept hibernating *Antrozous pallidus pacificus* throughout the winter. Alcorn (1944) reported finding several *Antrozous p. pallidus* in crevices in a mine tunnel in Nevada.

Spring and Summer Behavior and Habitat Selection

Habitat Selection

Myotis. The transition from hibernation to feeding appears to be gradual, partly dependent upon the temperature of the caverns and partly dependent, it is suspected, upon the amount of food available. Myotis begin moving out of Cavern IX in numbers in late March and early April. These bats disperse to warmer caverns where they congregate in large clusters or in crevices. These bats may or may not fly and feed in the evening. This is probably dependent upon the temperature of the caverns and the metabolic rate of the bats during the time they sleep, and the irritability of other bats in the cluster.

At Cavern VIII, small numbers of Myotis were present in the crack at VIII-B (Fig. 2, VIII) at the end of March. On April 10, 1953, this crack, in which Antrozous hibernate, was packed with hundreds of Myotis and remained filled until May 20. A cluster of an estimated 220 Myotis was found on the ceiling at VIII-C (Fig. 2) on April 10. On April 15, there were no Myotis at VIII-C, but on April 24 a single large cluster containing an estimated 1,000 bats was at the same place on the ceiling at VIII-C where the previous cluster had formed. On May 4, there were only 24 Myotis here, but on May 13, there were two large clusters consisting of an estimated 1,900 in one and 1,000 in the other. It was determined from banded bats captured that at least some of these came from Cavern IX. On the afternoon of May 19, an estimated 7,500 Myotis were active and clustered at the same place. These remained until the end of May at which time Cavern VIII was deserted by all Myotis. The climatic fluctuations in the cavern, for part of the time the Myotis were present, are illustrated by Figure 12, VIII-C. A pile of guano beneath this place began to accumulate in April and had become quite large by the time the bats left the cavern.

Many male Myotis are associated with Tadarida in Cavern II from the time Tadarida return in April until they leave in late October. These males cluster with the Tadarida at II-S and II-T (Fig. 2, II). When the Tadarida are frightened, they fly and form clusters in other parts of the cavern (II-Y, II-Q, and II-A). Myotis associated with the Tadarida fly with these bats and join the new clusters they form.

The clustering behavior of Myotis after feeding during the night seems to result in the formation of large clusters in warm places rather than many small clusters in cold places. Although the body temperatures of Myotis found singly during the feeding season approximate the ambient temperatures, the temperatures of those in clusters during these times are higher than the ambient temperature, the opposite of that condition in the winter. This can be explained on the basis that the warmer places the bats select necessitate a higher metabolism, thus causing all of the bats to be in an irritable state.

Awakened Myotis in spring and summer clusters do not fly as do those in winter clusters. Instead, they crawl and squeak and thus disturb other bats in the cluster so that the awakening reaction in these is also triggered. Consequently, many bats in a summer cluster have much higher body temperatures than that of the environment, and thus a higher level of metabolic activity than if they hung singly and assumed the temperature of the environment. The warmth from the awakened bats would seem to warm other members of the cluster still asleep.

The higher temperatures within the spring and summer clusters suggests that perhaps when feeding the cluster serves as a heat-conserving unit as the heat of metabolism would be lost to other bats, but which would, in turn, tend to warm the whole cluster. Digestion presumably would proceed more efficiently at these warmer temperatures, so that coupled with selection of warm habitat after feeding, the cluster formation serves to help the members of the cluster to digest their food.

When adverse weather conditions, such as thunderstorms, keep Myotis from getting food in the summer, it has been found that they usually cluster in the cooler parts of the caverns and assume deeper torpidity as in winter hibernation. The selection of cold or warm parts of the cavern by Myotis seems to be dependent upon whether or not the bats have eaten. It is well known that after a mammal has eaten, peripheral circulation is reduced and much of the blood is shunted to the stomach. A possible explanation of the observation that warm places are selected after feeding is that, due to the increased amount of blood in the viscera and the decreased peripheral circulation, the animal feels cold and selects a warm place to hang. Conversely, it is suspected that cooler places are selected after flying and not feeding, since peripheral circulation would not be reduced to such an extent and it is in these cooler places that the bat feels more comfortable. Such a system of metabolic conservation of energy would be of much value to bats.

Corynorhinus. Corynorhinus begin moving to the warmer parts of Cavern II in the first part of April. As spring and the feeding season progresses, small numbers of these bats arrive here from other winter quarters until, in June, several hundred individuals are present. After feeding, these active individuals are usually in the high, warm places at II-A, E, W, V, and X (Fig. 2, II). Females during the period of reproduction usually cluster at II-E. Males, on the other hand, remain solitary, seeming to hang in particular places in the cavern, to which, once frightened, they will soon return. No evidence of territoriality was noted, however.

Antrozous. Antrozous were not found from the time they left Cavern VIII at the end of March until they were rediscovered in a barn in Aetna, Kansas (Fig. 1, X), on May 19. These bats were not present in this barn on May 5. Antrozous in the barn occupy a crack one inch wide against the cement wall of the south side of the barn between the first and second stories. They rest with their bellies against the cement. When first discovered, a number of these bats were in a pile of boards on the floor adjoining this crack. The temperature in this crack from May 19 until August 7 when the bats were still present varied from 40.5° C. to 19.0° C. A thermohumidigraph record (Fig. 12, X) shows the daily climatic fluctuation near the crack for one week.

Eptesicus. A very few Eptesicus were found during the spring and summer. These were mostly solitary males in Caverns II and IX. These were found either hanging from walls or were in crevices similar to those in which they hibernate. Three males, found in May in small cracks outside of Cavern XI, were exposed to daylight. These same crevices contained Eptesicus in July. It is not known whether these were the same bats although numbers of feces in the crevices indicate that Eptesicus had been using them previously. A banded male Eptesicus was seen in the barn at X many times in June and July. This bat was always at the same place on a rafter near the roof at the south side of the barn. This suggests that male Eptesicus utilize the same places while resting during the spring and summer months. No female Eptesicus were found in the caverns in the spring or summer. Temperature measurements indicate that Eptesicus live in warm places during the summer although two exceedingly fat males were found at Cavern II-K (Fig. 2) in a very torpid state in this cooler part of the cavern in July during a period of hot weather.

Light-Sampling Behavior

Myotis. A large colony of Myotis was not available for study in June. After they disappeared from Cavern VIII, they were seen nightly flying east from somewhere west of that cavern. Cavern VII, where an estimated 15,000 to 20,000 adult Myotis spend the summer, was not discovered until July 8, 1953. Records from bands indicate that many in this cavern had been in Cavern IX during the winter. No other species of bats were seen in this cavern in the summer.

The Myotis in Cavern VII form three large clusters in as many rooms. Each of these clusters contains males, females, and young. There is very little air circulation in this cavern in the summer as evidenced by the thermohumidigraph record (Fig. 13, VII).

All members of the clusters are active and able to fly at all times of the day indicating that body temperatures are over ten degrees Centigrade higher than that of the rock. When evening approaches, the bats in the clusters begin squeaking loudly. Fifteen minutes before the first bats emerge from the very small entrances of the cavern, bats can be seen to fly into the light zone and turn around and fly back into the cavern. As the illumination from the sky decreases, bats fly farther and farther towards the outside until, about

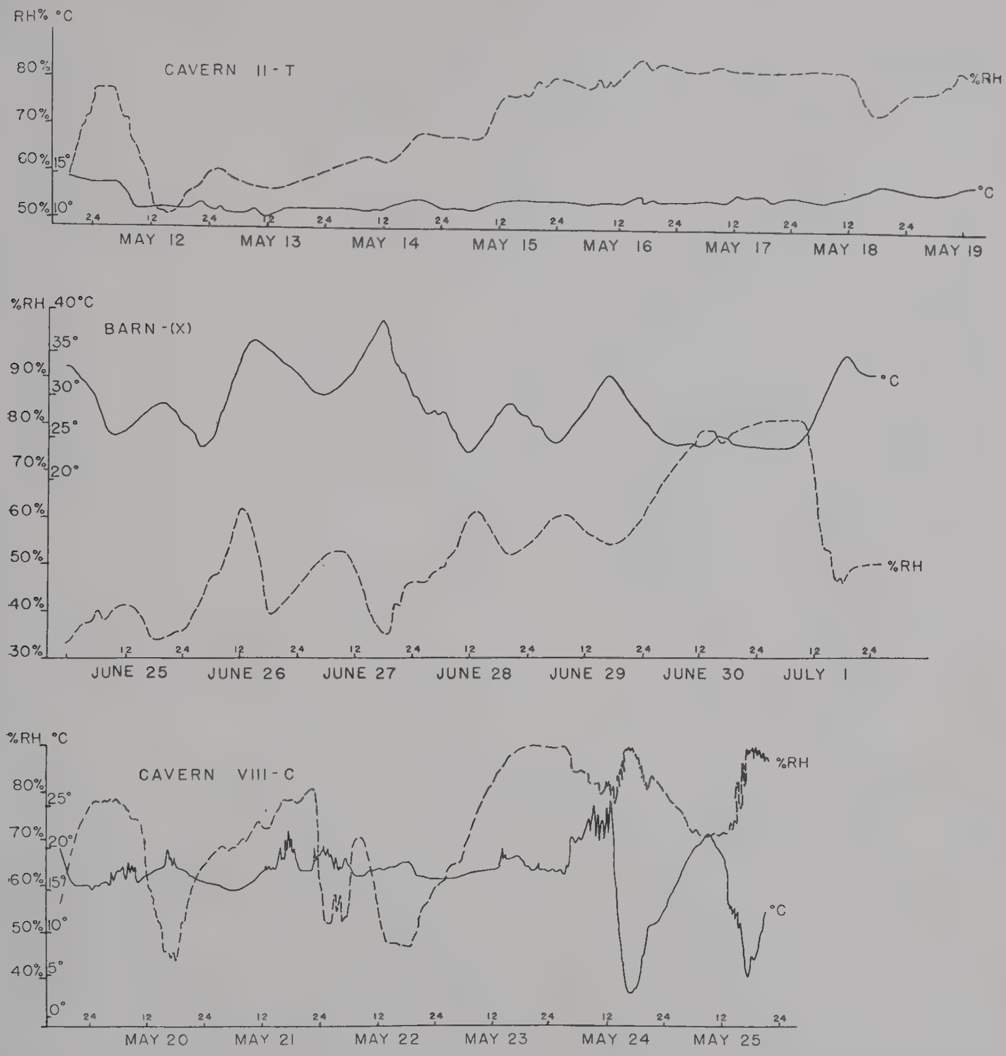

FIG. 12. II-T is a thermohumidigraph record showing climatic fluctuation beneath the clustering place of active male *Myotis* and *Tadarida* in Cavern II. X shows climatic fluctuation during the time that most members of a large colony of *Antrozous* gave birth to their young The instrument was placed one foot from the crack that the bats inhabited. VIII-C shows climatic fluctuation in Cavern VIII within five feet of a large, active, spring cluster of *Myotis.*

five minutes before they emerge, the vertical openings are filled with milling Myotis. About two minutes before emergence, one or two bats fly out for a distance of approximately ten feet and then return to the cavern. A few seconds later, other bats fly even farther from the entrance and as time progresses some make a circle about 30 feet in diameter before going back into the cavern. About 30 seconds before the time of emergence, a number of Myotis are making flights up to 50 yards away before returning to the entrance. At this time, several hundred bats leave the cavern and begin feeding, generally flying in an easterly direction. The number of bats leaving the cavern gradually increases until there are hundreds of bats leaving the entrances each minute about five minutes after the flight has begun. After the flight commences, very few bats turn around and go back into the cavern as they do when it is lighter. Usually, 30 minutes after the flight has begun, all of the Myotis have left the cavern.

This behavior is clearly that of light sampling.

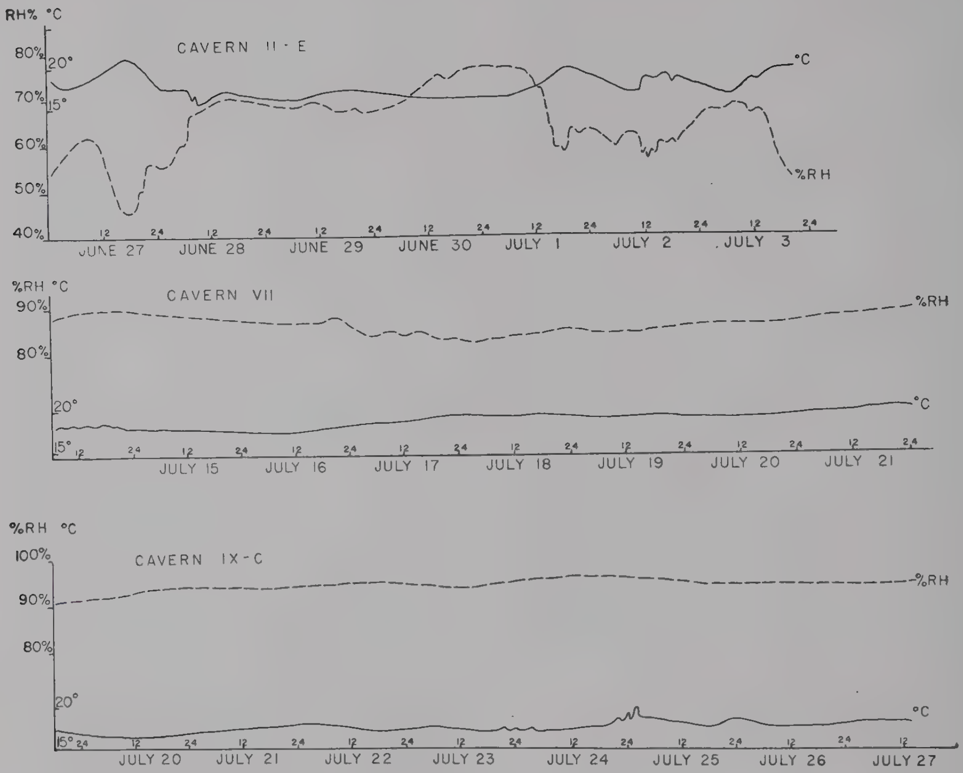

FIG. 13. II-E shows climatic fluctuation within ten feet of a brood cluster of adult female and young *Corynorhinus* in Cavern II. VII shows climatic fluctuation in Cavern VII where an estimated 10,000 baby *Myotis* were born and raised. IX-C shows the characteristic summer climatic fluctuation in Cavern IX.

Thermohumidigraph records inside and outside the caverns show that there is little or no temperature change during this period of twilight which Guthrie (1933) suggested might be the factor that brings bats out of caves in the evenings. The contention by Allison (1937) that Tadarida in Carlsbad Caverns leave after sunset when differential temperatures cause air to rush into the caverns is shown not to be true in these caverns; greater wind currents, which cause temperature and humidity fluctuations, are shown to be nonexistent at sunset by the thermohumidigraph data. This is illustrated by Figure 13, VII for Cavern VII and by Figure 12, II-T for Cavern II which is a thermohumidigraph record for temperature and humidity changes directly below the clustering place of a large colony of Tadarida. These bats exhibit the same light-sampling behavior as Myotis.

Table I shows the relationship of light intensity to time of emergence for Myotis. Sunset times for this table were computed from the *Nautical Almanac*. The three observations in May indicate that Myotis may come out slightly later after sunset early in the season than during July and August. Venables (1943) stated, regarding time of emergence of *Pipistrellus pipistrellus* in England, that it occurred around sunset in August and became progressively later towards either end of the season. Eisentraut (1952) found that *Pipistrellus pipistrellus* and *Eptesicus serotinus* in Germany came out slightly earlier in August and September than in June and July. He also stated that although no photometer readings were taken, that light was undoubtedly the factor determining the time of emergence.

The emergence of some of the Myotis from Cavern VII six minutes before sunset on August 2, a dark and stormy evening, and at sunset instead of later on the relatively clear evening of August 3 suggests that perhaps the factor of hunger overcomes their aversion to bright light. A heavy rain fell throughout the night of August 2 beginning at 8:30 p.m. making it improbable that

TABLE I. *The time at which the first* Myotis *left a cavern for evening feeding in relation to light intensity*

Date	Cavern	Time of emergence of first bat	Weston reflected light reading	Foot-candles	Minutes before (*) or after (–) sunset	Sky cover
22 May	VIII	1957	4.8	17	–19	Clear
23 May	VIII	1958	—	—	–20	Clouds in E.
25 May	VIII	1957	—	—	–17	Few cl. in W.
6 July	IX	1959	—	—	–5	Rainy
7 July	IX	2009	—	—	–15	Clear
8 July	VII	2000	—	—	–7	Cloudy
13 July	VII	2003	9.0	36	–11	Clear
16 July	VII	1946	10.0	40	*4	Cloudy
19 July	VII	1958	9.0	36	–11	Few cl. in W.
21 July	VII	1958	6.5	26	–10	Clear
24 July	VII	1956	9.0	36	–10	Clear
25 July	VII	1959	4.8	17	–13	Clear
26 July	VII	1956	6.5	26	–11	Clear
29 July	VII	1952	6.5	26	–9	Clear
31 July	VII	1948	9.5	38	–7	Few cl. in W.
2 August	VII	1934	9.0	36	*6	Stormy
3 August	VII	1939	18.0	68	0	Few cl. in W.

many of the bats fed successfully. The return of the bats to the universally warm quarters at Cavern VII that same evening would necessitate a rather high metabolism until the next evening. A small colony of 400 Myotis which was in Cavern IX during this time moved from a warm place 35 feet inside the entrance at IX-A (Fig. 2, IX-A) to a relatively cool place to the north of IX-C. These bats remained torpid for two days, whereas those in Cavern VII were active on August 3. The climate at IX-C during this time was about 5° C. cooler than that at Cavern VII. It is conceivable that a lower metabolic rate due to cooler caverns in the spring and fall reduces the hunger drive and thus the bats come out later. It is possible that the amount of light that does not dazzle the bats' rod-vision type of eyes is the factor which determines the earliest time of emergence and may be an explanation of the light-sampling behavior mentioned previously.

Behavior within the cavern before time of emergence is similar to that observed at the entrances. An hour to 20 minutes before the first bat leaves the cavern, one or two Myotis leave the loudly squeaking clusters. These fly to one of the rooms near an entrance and turn around and fly back to the cluster. The number of flying bats gradually increases within the cavern until, at the time of emergence, the cavern is filled with flying bats, many going to the dim light at the four small entrances from which they emerge.

Griffin and Welsh (1937) found that *Myotis l. lucifugus* and *Pipistrellus s. subflavus* kept in total darkness under constant conditions became active around sunset regardless of the time of feeding, which was at irregular intervals. One bat in their experiment, however, did not conform and showed an activity rhythm which began at the time of the first feeding which was not in the evening. The periodic behavior described by Griffin and Welsh helps explain the activity of Myotis at Cavern VII and elsewhere before coming out to feed.

The information on the behavior of Myotis within the cavern before going out to feed was obtained by sitting quietly in the cavern and watching the bats with a red light. When bats fly together in large numbers within the caverns, they apparently do not use their echo-location mechanism. Since there may be hundreds of flying bats within a small space, the number of voice sounds would seem to make such echo-location impossible. When standing in the line of flight a stream of Tadarida leaving Cavern II (near the entrance at II-Z, Fig. 2) with a headlamp focused on the oncoming stream, it was found that the Tadarida would dodge the area around the light. When standing in darkness, a number of flying bats would hit the observer. With one, two and three layers of red cellophane over the lens of the headlamp, the flying Tadarida continued to dodge the light. With four layers of red cellophane on the lens, however, the bats would behave as in total darkness. Flying Myotis often run into one another when they are confined in a small space as in Cavern VII. They do not run into the walls, however. This information indicates that under certain conditions echo-location is not used; their memory of the topography of the cavern is good; and they apparently do not see a red light.

Corynorhinus. Similar light-sampling behavior has been observed in Corynorhinus and Antrozous. Corynorhinus in Cavern II fly to lateral depressions in the cavern at points P and R (Fig. 2, II) from elsewhere in the cavern in the evening. Their light-sampling behavior differs from that of Myotis in that they fly to the entrance near P and return to the depression in which they had been hanging previously and hang for a few minutes before sampling the light again. These bats do not leave the cavern until it is dark.

Antrozous. The light-sampling behavior of Antrozous consists of their leaving the crack where they spend the day and flying around inside the barn. This behavior begins after sunset. As darkness approaches, the amount of light is evident through cracks in the barn and several individuals may crawl through the small openings at either the northeast or southwest corners where the Antrozous leave and return to the barn. If too light, they will back up and resume flying around the barn. Before they emerge from the barn, many Antrozous are flying about inside the barn although some are still present in the crack. During this pre-emergence flight, many alight on rafters near the ceiling at the north and south end of the barn. These places also serve as night roosts as described for *Antrozous pallidus* by Orr (1954). When the light intensity is about four foot-candles, several Antrozous leave the barn, fly around it once and return to the barn. As it gets darker, the bats that fly out of the barn circle it three or four times and then go back into the barn. When the light intensity is around one foot-candle (2.0 to 0.5 foot-candles according to measurements taken three times in June and July), the Antrozous begin leaving the barn one by one. These bats do not circle the barn as do those leaving earlier. Orr (1954) found that Antrozous in California did not leave their day roosts until the light intensity was less than one foot-candle.

Night Behavior

Myotis. Upon leaving Cavern VII in the evening, some of the Myotis fly up and down the many canyons feeding at tree-top level. The majority, however, fly east and northeast to a stream (Fig. 1) where they have been seen to drink. When making this flight, the bats feed at a height of 15 to 20 feet. No Myotis fly towards the west until light readings in that direction are less than 40 foot-candles. The cruising speed of Myotis has been determined by automobile speedometer to be 13 to 15 miles per hour when there is no wind. By 11:00 p.m. many of the Myotis have returned to the same places in the cavern where they spend the day, and by 2:00 a.m. the cavern is filled with bats. A morning flight seems to begin after this time, but there is no direction to the flight, the majority feeding near the cavern. As it begins to get light, numbers of Myotis can be seen flying towards the cavern from the east although most of the bats are back in the cavern by this time. These returning bats fly towards the cavern and into the entrances without hesitation. The number of returning bats greatly decreases until, as it gets light, there are very few returning. The light reading when the last bat returned to the cavern in July was 16 foot-candles on one occasion and 19 foot-candles on another.

Antrozous. The behavior of Antrozous after leaving the barn is to fly from three to six feet over the ground and to feed on flying insects. On two occasions, these bats were seen to alight on the ground and catch a crawling beetle which had been attracted to a nearby light. After 30 minutes, some return to the barn where they congregate in night roosts on high rafters at each end of the barn. The wings of cicadas are found in the guano beneath these roosts indicating that larger food is brought back to the barn to be eaten. A female Antrozous in captivity took six minutes to devour a cicada. Females with young have been seen to return to their young which are deposited on the wall before flying out of the barn and crawl into the crack where all of the Antrozous spend the day, rather than joining the bats at the night roost. Orr (1954) found that Antrozous fly early in the morning to feed after being at the night roost.

Corynorhinus were not observed after leaving the cavern in the evening.

Reproductive Behavior

Myotis. Two pregnant female Myotis were found torpid, hanging singly, in Cavern VI on June 25, 1953. No other bats were in the cavern. These were put in a large, warm cage and on the night of June 26 both gave birth to a single young. The birth process was observed in one of these Myotis. Instead of hanging head-upwards as has been reported for many vespertilionid bats where parturition has been observed, this bat hung head-down with its ventral side against the burlap side of the cage. The bat was in the beginning stages of labor when first observed; the time of birth took 20 minutes. The presentation was breech and the baby was caught in the folded tail membrane which was curled, the tip touching the belly. The female did not dress the young which crawled to a nipple by itself and began to nurse while the umbilical cord was still attached.

Female Myotis were caught carrying their apparently newborn young in Cavern IX on the night of July 3, but by July 6, nineteen of them had hung their babies at IX-C (Fig. 2, IX) while they went out to feed. This indicates that the young are carried only one to three days after birth. The period of birth in 1953 was between the last week in June and the first two weeks in July. Myotis continued to hang their babies at IX-C when they went out to feed in the evening until July 11 when two inches of rain fell. Water droplets form on the ceilings of many caverns after rain. Whether this is due to seepage or to condensation or both is not known. After the rain, the baby Myotis in Cavern IX were moved from IX-C where the ceiling was wet to a place 15 feet north of IX-C where the ceiling was dry. An indication of the summer climate in Cavern IX is shown by Figure 13, IX-C. That Myotis with young seem to select places with a constant, relatively high temperature and a high humidity is shown by this figure and by Figure 13, VII, for Cavern VII. In Cavern VII, after the rainstorm on July 11, an estimated 5,000 baby Myotis were moved from a room where there was water on the ceiling to rooms with dry ceilings. Five babies were not moved, however, and these died within two days. This suggests that their mothers had not returned from the night's foraging.

Eisentraut (1936) found that *Myotis myotis* recognized their own young whereas Casteret (1938, 1939) found that they did not, but rather the females would nurse any young. Observations from this study indicate that the young may try to nurse any female, but that the females do recognize their own young. This has been ascertained by observing the behavior of females that have been disturbed and come back to their young to move them elsewhere in the cavern. They will alight on the cluster of young at approximately the place from which they were disturbed and nuzzle many of the babies until apparently they find their own. At this time, they crawl over it and with their noses push the baby until it attaches itself to the mother with the claws and teeth. The female then flies with the baby to another part of the cavern.

The development of the clustering instinct is apparently a gradual phenomenon. When Myotis are very young, they are spaced throughout the cavern ceilings where their mothers have left them although they are able to crawl about the ceiling. As they grow older, they begin to form clusters, and by the time they have their juvenal pelage they form the same type of tight clusters as the adults.

Corynorhinus. The young of Corynorhinus are apparently born in Cavern II from about the 15th of June until the second week in July. After the young are a few days old, the females hang them on the cavern ceilings before going out to feed. Large clusters of female Corynorhinus with young are most often found at II-E (Fig. 2, II). This is the highest part of the cavern and was formed by a slab of gypsum over 100 feet in diameter falling in. The height from the ceiling to the top part of this rock varies from 18 inches to four feet. That this is a dry, warm location is shown by the thermohumidigraph record (Fig. 13, II-E). Pearson, Koford, and Pearson (1952) pointed out that lactating females selected warm places and that the growth of the young in cool places was much slower than in warm ones. The formation of large clusters at this time of the year, which does not seem to occur at other times, probably serves to keep the body metabolism of the young at a high rate as the females are active at all times of the day.

When disturbed, the females move from the seemingly preferred place at II-E to II-D, O or W. These are also warm, high places. The behavior of these bats when moving from one place to another is to fly in a rather tight group to the next place of clustering. Squeaks coming from the newly formed cluster seem to attract the few laggard individuals. Cornynorhinus seem to know their own young as Pearson, Koford, and Pearson (1952) showed for the California race of this species, and which is substantiated by behavior observed in this study. Their behavior of encouraging only their own young to nurse is similar to that described for Myotis.

Antrozous. Twelve pregnant Antrozous caught on June 24, 1953, from the barn in Aetna, Kansas, obviously, from the two distanct swellings, contained two embryos each. Two of these females were kept in a warm cage and on June 25 one of them gave birth to a male and a female young as did the other on June 26. Both gave birth to their young while lying on the floor of their cages. The female seems to aid in the birth by pulling on the fetus with her teeth.

The colony of Antrozous at Aetna contained an estimated 150 adult females and 50 males at this time. The first babies in the barn were seen on June 27. Most of the females had parturated by July 4. All that were observed had two young, although Orr (1954) reported that an occasional single or triple birth occurs in *Antrozous pallidus pacificus*. Females apparently carry their young with them when they go out to feed for only the first day or two; after that time, they deposit them on the cement wall above the crack where they spend the day, or on the side of the wall at the north end of the barn. A few individuals deposit their young in rectangular cement depressions in the wall on the first floor of the barn. After returning from the first night feeding, the females return to the group of young on the wall and inspect each one until they find those that are apparently their own. When the female finds one of her young, she crawls over it and picks it up in a pocket made by the base of the wing membrane and the elbow. The young is assisted by the mouth of the female. When very young, the babies are scattered over the wall, but as they grow older they begin to form clusters. Climatic fluctuation in this barn during the time that many babies were born is shown by Figure 12, X.

WEIGHTS

Bats were weighed in this study for the purpose of determining the effect of habitat selection on metabolic demands as reflected by weight loss during the hibernating season. The weight records for Myotis (Fig. 14) show that weights around the first of October are somewhat lower than in the middle or the end of October. Figure 14 indicates that weights decreased more rapidly from November to December than from December to February. The ambient temperatures at which Myotis were found (Fig. 5) show a sharp decrease from November to December and a leveling-off from December to February. An effect of temperature on weight loss and thus metabolism is indicated. The figures for the mean weights of Myotis in Figure 14 were determined on the basis of ten specimens or more for each sex and age group. Large samples of Eptesicus and Corynorhinus were not available for weighing, but those that were weighed, when plotted, show the same pattern as for Myotis (Twente 1954b).

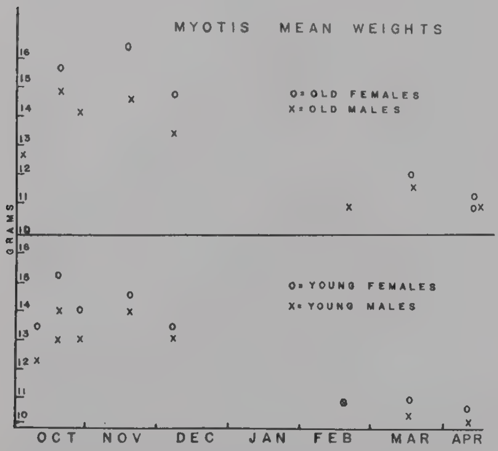

FIG. 14. Mean weights of *Myotis velifer* illustrating differences in weights of males and females and of old and young bats at different times during the hibernating season. "Young" bats are those in which tooth wear was negligible.

At the beginning of October, most of the Myotis in Cavern II selected warmer places, whereas during the latter part of that month the lower and cooler places were selected, the body temperature of the bats at these cooler places being much lower than those which were still active. It is conceivable that the increase in weight during early October, when insects are still plentiful, is due to the decreased metabolic activity during the day since cavern temperatures are becoming universally cooler at this time of the year.

DISCUSSION AND SUMMARY

This study of cavern-dwelling bats was made in gypsum caverns in south-central Kansas and northwestern Oklahoma. It was undertaken in an effort to ascertain habitat selection behavior and the effect of environmental changes on this and other behavior of *Myotis velifer incautus, Corynorhinus rafinesquei pallescens, Antrozous bunkeri,* and *Eptesicus fuscus pallidus.*

Some hibernating bats are sensitive and awaken with little provocation. The awakening reaction of others, whose body temperatures were the same, could be triggered only by relatively violent disturbance. Once the awakening reaction of a torpid bat has been triggered, a constant and rapid temperature rise continues until the bat reaches a body temperature at which it is capable of flight. This is interpreted to mean that the "degrees of torpidity" of other authors are actually degrees of irritability which are directly related to the area under the time-temperature curve of a sleeping bat, and consequently to the amount of stored food that has been catabolized. It is postulated that the irritability of a resting bat may be dependent upon the amount of urine in the bladder and the nervous consequences of a partly extended or extended bladder, and that it is these factors that cause awakening after a period of time in a torpid state.

The temperature of the air near the gypsum and the temperature of the gypsum of the caverns studied is colder, due to the evaporation of ground water, than that of the air from the outside which circulates through the caverns. The body temperature of torpid bats approximates the temperature of the rock except where warmer air currents disturb the layer of cold air next to the rock. In these instances, the body temperature of a bat approximates that of the circulating air. When in dense clusters in the winter, the temperatures of bats within the cluster are lower than those on the periphery since those in the center are not washed by currents of warm air. This implies a lower metabolism of bats in the center of the cluster than those on the periphery, and thus a lesser degree of irritability after a period of time in a torpid state. The function of clusters in the hibernating season, therefore, is to keep the bats cold and thus conserve metabolic energy. It has been found that when bats are not feeding that they select the cooler parts of the cavern in which to go to sleep.

When bats have been feeding, however, it has been found that they select the warmer parts of the cavern in which to rest. The higher body temperature, which results from hanging in a place with a relatively high temperature, would seem to facilitate digestion. The function of clusters during the feeding season appears to be the conservation of heat, and to keep the animals warmer than the environment. Bats in summer clusters do not fly when they awaken as do those in the winter. Since bats hanging in warm places are likely to become irritable after a short period of time, some bats in the cluster awaken and attain a high body temperature. These awakened bats disturb and trigger the awakening reaction of other sleeping bats. The result of this activity within the cluster tends to keep the temperature of the bats in the cluster somewhat higher than that of the surrounding air. The body temperatures of those bats which are not awakened would seem to be raised by the heat released by the awakened bats.

The function of clusters under different conditions appears to be dependent upon the temperature of the place at which the cluster forms and consequently the degree of irritability of the bats within the cluster.

The generally cooler temperatures in the caverns in the fall and the lower metabolism of the bats would seem to explain the sudden increase in weight which bats exhibit at this time. Digestion and assimilation of a relatively small amount of food, when the body metabolism was low, would allow for a build-up of fat reserves which would not be possible if a high metabolism were maintained.

Another factor which appears to be of importance in the hibernating season is the morphological characteristics of the walls and ceilings which the bats select. Corynorhinus, in the hibernating season, usually are found hanging singly on very rough walls; Eptesicus in small horizontal crevices; Antrozous in colonies in protected cracks; and Myotis in clusters on ceilings of variable conformation. The very rough walls where Corynorhinus are usually found tend to break up air currents and consequently pockets of cold air remain around the bats which are therefore not warmed by the circulating air. In addition, the hibernating posture of Corynorhinus insulates against the warm air. The narrow crevices selected by Eptesicus remain quite cool and are little affected by circulating warm air. The cracks selected by colonies of Antrozous serve a similar purpose of protecting the bats from warm air currents.

It has thus been shown that although the habitat selected by the four kinds of bats is generally different, the end result of selecting places that best suited their metabolic needs was accomplished. However, the hibernating habitat selected by all of the bats, except Antrozous, was by no means always suitable. Habitat selection of cavern-dwelling bats in the winter seems to be partly a trial-and-error system. It has been found that the bats, with the exception of Antrozous which stays in the same crack, awaken throughout the winter and move to a different place within the same cavern or move to another cavern. Those hibernating bats that hang in unfavorable (warm) places become irritable and move in a shorter period of time than those in cooler, more favorable places. The favorableness of a hibernating site may be dependent upon the amount of wind blowing by it which disturbs the layer of cold air next to the rock. Windy places are generally avoided although the amount of circulating air depends on the direction and force of the wind outside the cavern. Consequently, a place selected may be suitable for a short period of time, but a shift in wind direction may make currents of warm air blow over the bat and thus increase its metabolic rate which, in turn, makes the bat irritable and, thus, eventually awaken and move.

This passive means of selection of habitat coupled with the active means of selecting temperature and certain types of surfaces on which to hang is particularly striking in bats, which are especially metabolically responsive to environmental changes. Similar means of habitat selection, which are, in certain respects, more trial-and-error than might be expected, are probably utilized by many animals.

The social behavior of clustering does not seem to limit population size, as does aggressive behavior, but rather it appears to favor survival of all of the members of the population by moderating the temperature of the bats within the cluster so that their metabolism is suited to their needs at the time. The behavorial responses to environmental changes are largely passive and are directly related to the metabolic rate.

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HETEROTHECA LATIFOLIA, A NEW AND AGGRESSIVE EXOTIC DOMINANT IN PIEDMONT OLD-FIELD SUCCESSION

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Introduction

When farm land is abandoned in the Piedmont regions of the southeastern states, the land is thereafter occupied by a series of natural plant communities that show distinct changes from one stage to another (Oosting 1942). Crabgrass (*Digitaria sanguinalis* (L.) Scop.) usually is dominant is fields in the late summer and fall following cultivation. During the first year of abandonment, horseweed (*Erigeron canadensis* L.), a plant normally 4 to 6 feet tall, is the usual dominant. Horseweed is still present the following year, but the plants are less than a foot tall and are hardly noticeable among the 3 to 5 foot asters (*Aster pilosus* L.) that are usually abundant in such fields. The third year following abandonment, broomsedge (*Andropogon virginicus* L.) assumes dominance and maintains it until replaced by pines in 10 to 15 years. A climax stand of oaks, hickories, and smaller hardwoods replaces pines in less than 200 years. There are a few regular exceptions to this succession (Oosting 1942, Keever 1950). (1) Ragweed (*Ambrosia elatior* L.) regularly follows winter grains. (2) *Aster* shares dominance with horseweed in first-year fields when the last cultivation of the preceding year took place as early as June. (3) Ragweed, with *Diodia teres* Walt. and *Aristida dichotoma* Michx. may be the dominants in first- or second-year fields if erosion is severe. (4) *Aster* may hold dominance past the second year if water conditions are better than average.

Causes of changes in the early stages of old-field succession in the Piedmont of North Carolina were studied (Keever 1950) and it was concluded that the particular timing of the events in the life cycles of the first series of invaders and their relation to the season of year in which secondary succession is initiated, influences the rise and fall of dominant species more than changes in the environment. At that time, horseweed was the only species in the area studied, with the genetic possibilities of becoming a large plant, the timing of whose life cycle fitted the cultivational practices of the area in such a way that it could be the dominant in most first-year fields. The few exceptions to horseweed as the first-year dominant were caused by variations from the usual mid- to late-summer last cultivation of a field, or to other disturbances of the soil after that time.

Further investigations into certain phases of early old-field succession involving the use of horseweed fields were contemplated near Gaffney, S. C., in the fall of 1952. When an attempt was made to locate suitable horseweed fields, it was discovered that horseweed fields in the immediate area were difficult to find and that a species of *Heterotheca* was occupying such fields as are normally occupied by horseweed in the remainder of the Piedmont. Farmers reported that the weed had been present near Gaffney only 5 or 6 years and was becoming quite a problem. The weed looked somewhat like *Heterotheca subaxillaris* (Lam.) Britt. and Rusby, a plant common in the coastal plain of the southeast, which had not been reported from the upper Piedmont of the Carolinas. Many *Heterotheca* plants near Gaffney were more than 6 feet tall and showed a strong tendency to branch near the top, while *Heterotheca subaxillaris* of the coastal plain is a much shorter plant which usually branches profusely near the base. Not only the general appearance, but also the ecological behavior of the two plants seemed to be quite different.

Specimens of the questionable *Heterotheca* were identified by Lloyd H. Shinners as *Heterotheca latifolia* Buckley, which he says is an exceedingly common old-field or waste-ground weed in central and eastern Texas. The type specimen for this species was examined by Dr. Shinners in the Herbarium of the Academy of Natural Science in Philadelphia (Shinners 1951).[1]

Research was undertaken to determine the extent of the local distribution of *Heterotheca latifolia,* its ecological behavior, and its effect on old-field succession.

METHODS

Distribution

Heterotheca, with its numerous yellow heads, is quite conspicuous during most of September and October and can be easily recognized from a car moving at normal speeds. In the fall of 1952 and 1953, its general location in the area was estimated. Gaffney seemed to be near the northeastern limits, with Gastonia, Lincolnton, and Rutherfordton in North Carolina, and Rock Hill in South Carolina lying just outside its limits. The plant was abundantly present around Spartanburg, Greenville, and Union, South Carolina; it also was present at Athens, Georgia, and it was assumed that the two areas might be continuous.

During August, September, and October of 1954, the entire suspected area was checked carefully to find the exact limits of *Heterotheca latifolia.* Beginning at some fixed point within the area where the plant is abundant, fields adjacent to the major highways were checked for the presence and abundance of the weed. The location of the last plant in a given direction was determined and marked on a map. (Table I, Fig. 1.) Although the checking of the distribution of *Heterotheca* can be done more efficiently in September and October, it can be done with reasonable accuracy in August. In the Georgia area where the checking was done in August, every abandoned field along the highways in the transition area was carefully inspected by walking through it and looking for the presence of the plant. The South Carolina-North Carolina area was checked in September and October quite easily and accurately, as even one blooming plant of the species can be recognized across the full width of a field.

Inquiries were made of farmers in many areas as to when the plant was first noticed on their farms. Most farmers had not seemed to notice the first invaders, and had only become conscious of it when it became plentiful enough to be a nuisance on the farm; however, a few could tell the year when it first appeared on their farms and could give valuable information as to its behavior in the early stages of invasion.

Ecological behavior

Studies were made of the life cycle of *Heterotheca* by watching for time of blooming and mat-

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[1] The taxonomy of *Heterotheca* is in a state of confusion at the present time. A specimen Keever #1425) of the plant under consideration in this paper and identified by Shinners as *Heterotheca latifolia* Buckl. has been deposited in the Herbarium of Duke University.

TABLE I. *Location of the last plant of* Heterotheca latifolia *seen in fields adjacent to highways in 1954 in traveling way from areas of known abundant occurrence of the species*

Location number	Highway	Miles	Direction	From
1.....	U. S. 129	16.2	northwest	Broad x Lumpkin St. in Athens, Ga.
2.....	U. S. 29	38.4	northeast	Broad x Lumpkin St. in Athens, Ga.
3.....	U. S. 72	36.4	east	Broad x Lumpkin St. in Athens, Ga.
4.....	U. S. 78	35.6	southeast	Broad x Lumpkin St. in Athens, Ga.
5.....	U. S. 441	16.1	south	Broad x Lumpkin St. in Athens, Ga.
6.....	U. S. 78	9.8	southwest	Broad x Lumpkin St. in Athens, Ga.
7.....	U. S. 29	19.8	west	Broad x Lumpkin St. in Athens, Ga.
8.....	U. S. 76	0.8	south	S. C. 133 x U. S. 76 in Clemson, S. C.
9.....	U. S. 78	8.0	north	U. S. 78 x S. C. 183 in Pickens, S. C.
10.....	U. S. 25	7.5	north	U. S. 25 x S. C. 276 in Travelers Rest, S. C.
11.....	U. S. 176	0.4	south	U. S. 176 x railroad in Tryon, N. C.
12.....	N. C. 26	10.5	northwest	N. C. 26 x N. C. 182 in Polkville, N. C.
13.....	N. C. 150	4.4	northeast	N. C. 150 x N. C. 180 near Shelby, N. C.
14.....	U. S. 29	3.5	northeast	U. S. 29 x U. S. 29A in Grover, N. C.
15.....	S. C. 5	2.7	southeast	U. S. 29A x S. C. 5 in Blacksburg, S. C.
16.....	S. C. 9	12.8	southeast	S. C. 9 x S. C. 91 in Lockhart, S. C.
17.....	U. S. 76	0	0	U. S. 76 x U. S. 19 near Newberry, S. C.
18.....	U. S. 276	14.5	south	center of Fountain Inn, S. C.
19.....	U. S. 176	2.7	north	U. S. 176 x U. S. 178 near Anderson, S. C.

uration of seeds. Seeds were collected and tested for germination; seeds were planted and seedling growth and behavior noted in experimental plots and in natural fields.

In the fall of 1953, studies were made of number, size, and distribution of *Heterotheca* and other common old-field species by means of quadrats in 6 first-year fields, 3 second-year fields, and 1 fourth-year-field near Gaffney. In each of these fields, 10 quadrats ¼ x 1 meter in size were laid out along lines at evenly spaced intervals, from 15 to 45 feet apart, depending on the size of the field. All plants of *Heterotheca,* horseweed, *Aster,* ragweed, and broomsedge located in these quadrats were counted, and height measurements were made of *Heterotheca* and horseweed plants. Presence and abundance of other species were noted. Thirteen other fields were observed without counting quadrats. In these fields, the past cultivational history, the relative abundance and size of *Heterotheca* and other usual old-field dominants were noted.

RESULTS

Distribution

There are 2 distinct spots where *Heterotheca latifolia* occurs in the Georgia-Carolina Piedmont: one with its center a few miles east of Athens, Georgia, and the other with its center near Spartanburg, South Carolina. The Carolina spot is about 80 miles in diameter, with the South Carolina towns of Blacksburg, Chester, Newberry, Laurens, Williamston, Clemson, Pickens and Marietta, and the North Carolina towns of Tryon, Rutherfordton, Polkville, Fallston, Waco, and Kings Mountain marking the approximate limits. The Georgia area is about 40 miles in diameter with the towns of Elberton, Washington, Madison, Winder, Jefferson, Commerce, and Hartwell just outside its limits. Table I shows the location of the last *Heterotheca* plant seen adjacent to certain highways in traveling away from areas of known abundant occurrence of the species. Figure 1 is a map on which the locations indicated in Table I are connected to show the approximate limits of the two areas of *Heterotheca latifolia* in 1954. Within these areas, and to within 5 to 10 miles of the last plant in each direction, *Heterotheca* is the most abundant weed present. There is a transition area between those parts where the weed is abundantly present and the area surrounding the spots where the weed is completely absent. In the part of the transition zone nearest the center, there are occasional fields in which there are spots of *Heterotheca* usually about ⅛ of an acre in size. Near the outer edges of the transition zone, the small spots of the weed are less frequent and *Heterotheca* is seen occasionally as an isolated plant.

Farmers near Spartanburg say that the weed was first noticed there in the early 1940's, and its appearance is reported nearer the periphery of its present distribution at later dates. It has not been possible to check the exact time and place of establishment in South Carolina, and the rate of spread can only be estimated. General observations in the Gaffney area over a period of 3 years indicate that it is definitely spreading and that the rate of spread probably is between 5 and 10 miles a year. A farmer at Colbert, Georgia, a small town near the geographical center of the Georgia spot, claims to be the first person in that area to have noticed the plant, which appeared in a lespedeza field in noticeable numbers in 1948. It was not known to be present in Athens, Georgia, 12 miles from Colbert, in 1950, but it was recognized there in 1952.

Ecological behavior

Life cycle.—The first blooming *Heterotheca* plants were seen on the 5th of August and most plants were in full bloom by early September and continued to bloom past the middle of October. Mature seeds were found early in September and germinated immediately when placed in a moist

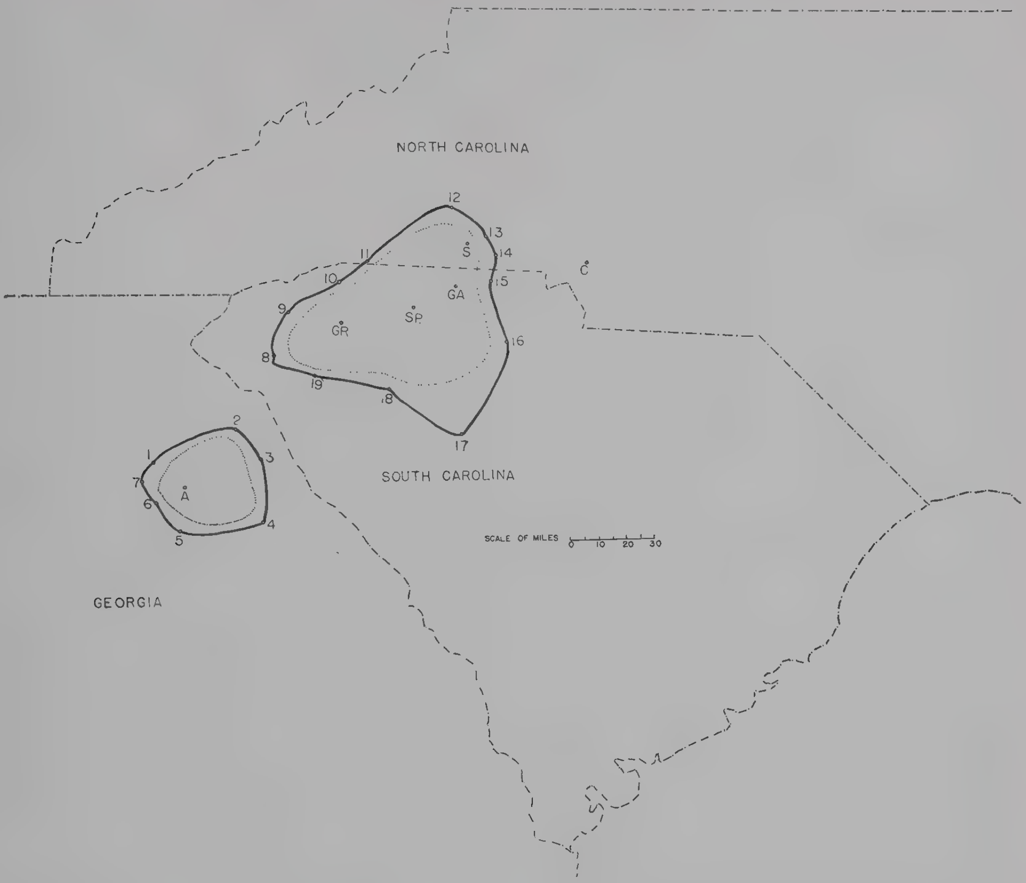

FIG. 1. A map of portions of Georgia, South Carolina, and North Carolina showing the location and extent of the two distinct spots of *Heterotheca latifolia* in the area. The numbers indicate the location of the last *Heterotheca* plant seen adjacent to certain highways in traveling away from areas of known abundant occurrence of the species, and correspond with the numbers in Table I. The solid line shows the approximate limits of the species in the area in 1954 and the area between the dotted line and the solid line is the estimated transition zone between the areas where the species is very abaundant and those areas where it is completely absent. A = Athens, Gr. = Greenville, Sp. = Spartanburg, Ga. = Gaffney, S. = Shelby, C. = Charlotte.

chamber. An abundance of seedlings is found in fields, roadsides, and any otherwise unoccupied soil in the fall. One field that had been plowed in the early spring of 1953 and abandoned immediately showed a full stand of *Heterotheca* in the fall of 1953, which indicates that the seeds that do not germinate in the fall may do so the following spring. The fall seedlings live over winter, grow in height the following spring and summer, bloom in late summer and fall, and then die. A few plants in Athens, Georgia, were observed to live over the mild winter of 1953-54 and bloom in the early spring of 1954, but no such behavior was noticed around Gaffney, S. C.

Quadrat counts—first-year fields.—Five of the 6 first-year fields studied by the quadrat method were clearly dominated by *Heterotheca*. The one exception, Field 4 (Table II), looked as if it might be dominated by *Heterotheca* when viewed from the adjacent highway in October, because the very large blooming *Heterotheca* plants in the field were more conspicuous than the more numerous horseweeds that were not as tall and were past their blooming period. Field 6 had a few more horseweed plants than *Heterotheca,* but the larger *Heterotheca* plants gave much more ground cover. Considering all 6 fields together, *Heterotheca* averaged 15.7 plants for each quadrat (¼m x 1m) and was present in 78 per cent of them. (Fig. 2). The tallest *Heterotheca* plant measured in the quadrats was 90 inches, and the average height of all *Heterotheca* plants was 36 inches. In the same

TABLE II. *Comparison of density (D), frequency (F), and average height of* Heterotheca latifolia *and horseweed* (Erigeron canadensis) *plants in 10 ¼m x 1m quadrats in each of 6 first-year fields*

Field number	Previous crop or treatment	Heterotheca			Erigeron		
		D	F	Av. ht. (inches)	D	F	Av. ht. (inches)
1......	cantaloupes	68.2	100	33	.8	30	29
2......	top soil removed	17.2	100	43	2.7	100	29
3......	corn	5.0	90	47	.7	30	29
4......	cotton	.4	30	62	4.7	90	37
5......	cotton	2.2	100	50	.7	60	31
6......	corn	1.1	50	58	1.4	90	41
	Average	15.7	78	36	1.8	67	35

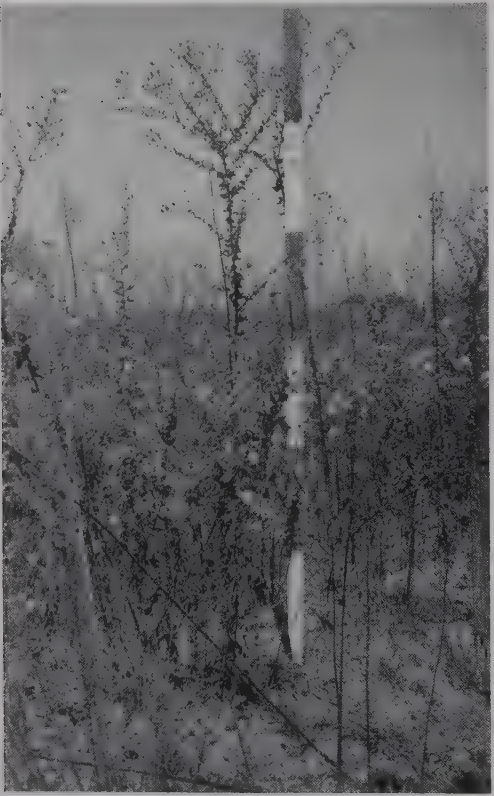

FIG. 2. Tall, top-branching *Heterotheca latifolia* plants in a first-year abandoned field with lower plume-topped *Erigeron canadensis.* The stake in the picture is 6 feet tall and marked at 1-foot intervals.

quadrats, horseweed had a density of 1.8, a frequency of 67, a height of 80 inches for the tallest plant, and an average of 34 inches for all plants measured. Although the average height of all *Heterotheca* plants measured was only a little more than the average height of all horseweeds measured, in the individual fields, *Heterotheca* always had the greatest average height. The difference between *Heterotheca* and horseweed size was more noticeable when the total density for both plants was low.

Young *Aster* plants 2 to 3 inches high (D,O.9; F,43) were present in all fields except the one following cantaloupes where the density of *Heterotheca* was very high (68.2). Ragweed was present as a distinct understory to *Heterotheca* in Field 5 and in eroded spots in the other first-year fields. *Lespedeza* spp. and crabgrass were present in some fields, at places nearly covering the ground. Other plants of the same species reported by Keever (1950) to be present in the Piedmont of North Carolina were also present in this area.

Quadrat counts—second-year fields.—*Heterotheca* does not replace *Aster* as the second-year dominant, but remains a much stronger component of the community than does horseweed in second-year fields in other places in the Piedmont. *Aster* plants were present in every quadrat counted in the 3 second-year fields and had a density of 8 plants for each of the ¼m x 1m quadrats, (Table III). The asters were about the same size as those commonly seen in second-year fields elsewhere. *Heterotheca* plants showed almost as high a density (7.9) as did *Aster* (8.0), but averaged only about 15 inches in height, forming an understory to the asters (Fig. 3) Only 2 small horseweed plants were counted in the 30 quadrats. Other plants in the second-year fields were quite similar in kind and number to those in second-year fields elsewhere.

Quadrat counts—fourth-year field.—No undisturbed third-year fields were found, so 10 ¼ x 1m quadrats were counted in a field that had been uncultivated and undisturbed for 4 years. In this field, an average of 7 mature broomsedge plants

TABLE III. *Comparison of density (D) and frequency (F) of* Aster pilosus *and* Heterotheca latifolia *in 10 ¼m x 1m quadrats in each of 3 second-year fields. The asters, most of which were about 3 feet high, were not measured*

Field number	Aster		Heterotheca		
	D	F	D	F	Av. ht. (inches)
7.........	3.4	100	8.5	80	19
8.........	14.2	100	.4	30	21
9.........	6.5	100	14.7	80	12
Average....	8.0	100	7.9	63	15

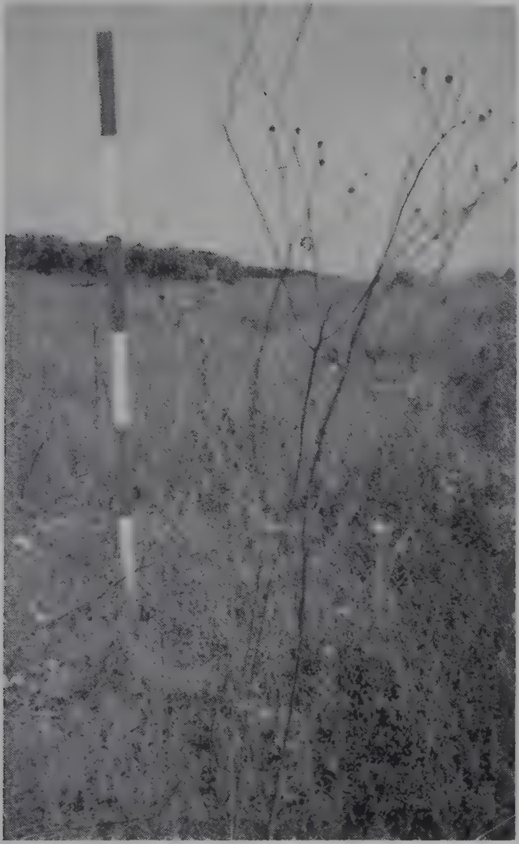

FIG. 3. A second-year abandoned field with small-flowered *Aster pilosus* and larger-flowered *Heterotheca latifolia* in approximately equal densities. *H. latifolia* is less than half as tall in second-year fields as it is in first-year fields. Most of the dead stalks are *H. latifolia* of the preceding year.

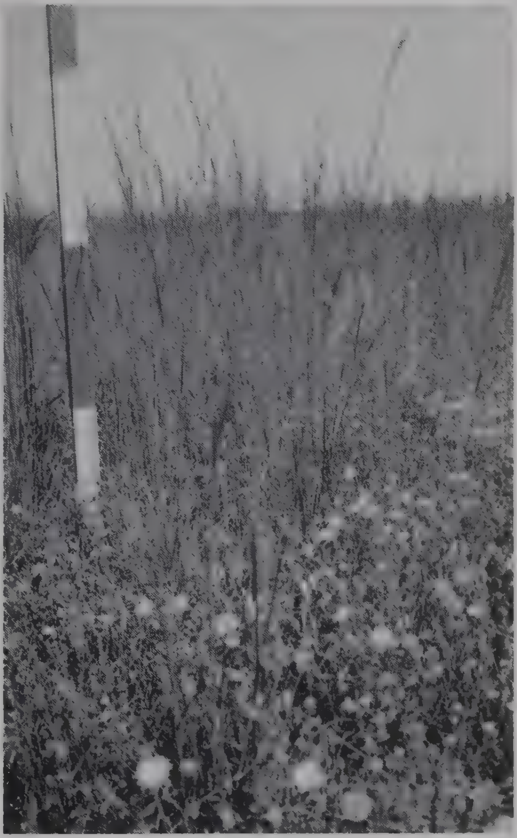

FIG. 4. A field 4 years after abandonment showing numerous small *Heterotheca latifolia* plants under broomsedge.

about 3 feet tall and 2.5 broomsedge seedlings were found in the quadrats. An understory of small *Heterotheca* plants was present under the broomsedge with a density of 14.7, and an average height of 11 inches (Fig. 4). Although this was the only undisturbed bromsedge field located and counted, other bromsedge fields of various ages and various conditions of disturbance continued to show this understory of *Heterotheca* until both broomsedge and *Heterotheca* were replaced by pines.

General field surveys.—Other fields besides those in which quadrats were counted were observed, past histories investigated, and behavior of *Heterotheca* noted. Of 8 fields which had been planted in winter grains, 5 were dominated by ragweed, 2 by crabgrass, and only 1 by *Heterotheca.* All of these former grain fields had scattered spots of *Heterotheca,* especially on the erosion control terraces and around the edges. Two fields had been plowed and planted in pasture grasses. In both cases *Heterotheca* had become established as the most abundant plant, and only a few scattered spots of pasture grasses remained. A peach orchard showed an interesting pattern of *Heterotheca* and *Aster:* between the trees there were spaces which had been plowed in March, and which were occupied in October by a full stand of very large *Heterotheca* plants; close under the trees there were areas which had only been mowed in the spring and which showed a full stand of *Asters* in the fall. One badly eroded field that had not been cultivated in 5 years was a spotty mixture of *Aster,* goldenrod, broomsedge, and young blackgum trees. In both *Heterotheca* areas studied in Georgia and the Carolinas, the plant was abundantly present on such uncultivated land as fields, ditch banks, roadsides, uncultivated erosion-control terraces, unkempt yards, pastures, and lespedeza fields. Farmers have little trouble with it in clean cultivated fields such as those planted in corn and cotton, but it is causing much trouble in fields and pastures where perennial plants such as pasture grasses and lespedeza are growing. In competition with these perennial plants, it does not attain the large size it does in first-year fields and other places with less competition, but it is almost impossible to eradicate. It is an annual, but each year a new and more dense stand appears.

CORRELATIONS AND CONCLUSIONS

Heterotheca latifolia, a plant common in Texas, has recently appeared in great numbers in two spots in the Peidmont of Georgia and the Carolinas and is spreading rapidly. Although a number of hypotheses have been advanced as to how the first plants got started in those areas, none has been proved. It is not uncommon for a plant native to one section to be introduced into another area, for seeds are easily transported as contaminants of commercial seeds, in hay, by railroad cars, and by many other means. Many plants have been known to thrive as well or better in the new locality as in the old one. It is quite possible that there are other places in the southeast, outside its range in Texas, where *Heterotheca latifolia* has become established. It is possible that the plant mentioned by Harper (1944) as being recently abundant in Birmingham, Alabama, might be the same thing. He says of *Heterotheca subaxillaris,* "A variable species, perhaps divisible into more than one. A prostrate form seems to be native on drifting sands on Dauphin Island, and Dr. Mohr reported it also from similar places in Baldwin County. Taller forms are seen occasionally in sandy waste places in the coastal plain, and in recent years one has been quite abundant in and around railroad yards in Birmingham."

It is somewhat unusual, however, to have the opportunity to study the behavior of such an introduced plant in the early years while it is still present in isolated areas, and while the effects of the advancing population of the introduced plant on the established vegetation can be observed.

The introduced *Heterotheca* is causing a distinct change in the early stages of succession on abandoned land in the areas where it is present. Before its arrival, horseweed was the undisputed dominant in fields which had been clean-cultivated the preceding year, the only exceptions being caused by some disturbance of the soil after late summer of the year of abandonment. Horseweed was the only large weed whose life cycle fitted the common cultivational practices of the region in such a way that it could become dominant the first year after abandonment. *Heterotheca* has the same timing of life cycle: both species bloom in the late summer and fall, they both live over winter as rosettes and grow to be tall plants the following summer, and they both attain their maximum size in first-year fields where the density of all plants is much lower than in the following years. Although both *Heterotheca* and horseweed are present in second-year fields in large numbers, they are smaller there than in first-year fields, and neither can compete successfully with *Aster* for dominance. With so many similarities, it might be assumed that the two species would be codominants in first-year fields. This is rarely the case, however, in areas where *Heterotheca* has been present a few years. *Heterotheca* is definitely replacing horseweed as the first-year dominant; as the new invader becomes more abundant, horseweed is becoming less numerous. This increase in number of *Heterotheca* individuals and decrease in number of horseweed is not taking place in oldfields only. Formerly, horseweed was consistently present in any sparsely plant-populated spot such as bare spots in yards, ditch banks, cracks in sidewalks, and such places. Now *Heterotheca* appears in such places and horseweed is seen there only occasionally. *Heterotheca* seems to have the genetic possibilities of becoming a slightly larger and more vigorous plant than does horseweed. When placed in direct competition with each other, as they are in first-year fields, *Heterotheca* outgrows horseweed. This larger growth could be of distinct survival value to the species; more *Heterotheca* seeds are produced than are horseweed seeds, and the following year still more *Heterotheca* plants grow in the old fields of the area. As this process continues year after year, *Heterotheca* numbers increase and horseweed numbers decrease, until the formerly most common weed of the area is being locally reduced to insignificant numbers.

SUMMARY

Heterotheca latifolia Buckley, a plant common in Texas, has appeared in two areas in the Piedmont of Georgia and the Carolinas within the past 15 years and is spreading rapidly. The Carolina area, which is approximately 80 miles in diameter, originated near Spartanburg, South Carolina, and now extends into parts of North Carolina. The Georgia area is about 40 miles in diameter and has a center a few miles east of Athens, Georgia. In both areas, the plant makes its most vigorous growth in first-year abandoned fields and is replacing horseweed as the dominant

in those fields. Although remaining an important component of old-field communities through the broomsedge stage, it does not replace the usual dominants of the region in stages later than the first year.

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A RESTING STAGE WITHOUT ENCYSTMENT IN THE ANNUAL CYCLE OF THE FRESHWATER COPEPOD *CYCLOPS STRENUUS STRENUUS*

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Resting stages are known to occur in the freshwater cyclopoids *Cyclops bicuspidatus thomasi* Forbes from North America (Birge and Juday 1908, 1911; Moore 1939; Cole 1953) as well as in *Cyclops leuckarti* Claus and *Cyclops bicolor* Sars (Fryer & Smyly 1954). Besides these species where the resting period is a more or less regularly recurring event in the annual cycle, cyclopoids have also been found in a dormant condition during periods of desiccation. Resting stages have further been found among a few species of freshwater harpacticoids as summarized by Deevey (1941). Encystment seems to be the rule in all except *C. leuckarti,* in which the resting stage occurs in winter.

A resting stage without encystment primarily confined to summer, was found by the present author in *Cyclops strenuus strenuus* Fischer from localities situated about 40 km NW of Oslo, Norway. The field studies were carried out in 4 small permanent ponds with depths less than 1 m and in a 5 m deep, eutrophic, stratified tarn, Bergstjern, 130 m long and 60 m wide.

The difficult taxonomy of the *C. strenuus* group made morphometric analysis necessary. By comparing some of the most critical indices with those of Kozminski (1936) and by following his table, the form investigated was found to be *C. strenuus strenuus* Fischer.

The outlines of the seasonal cycle of *C. s. strenuus* are fairly well known (Kozminski 1936) and the subspecies may be characterized as active during the cold season and disappearing from open water during summer. Reproduction occurs chiefly in early spring but may also take place in autumn and in winter. Little is known as to the details of the annual cycle, however, especially of events in summer. Gurney (1933) considered from samples in open water that summer might have been passed in copepodid stage V in a pond that dried up completely, whereas Herbst (1951) suggested that the subspecies may pass the summer in the egg stage. The present investigations show that *C. s. strenuus* spends the summer in copepodid stage IV, lying dormant in the mud without encystment.

Evidence of a Resting Stage

The following observations imply a summer resting stage without encystment:

1. Plankton samples collected at weekly or fortnightly intervals during autumn and spring show that activity in open water begins and ends primarily with the fourth copepodid stage (Fig. 1).
2. Bottom samples to which filtered tap water has been added produce individuals of copepodid stage IV within a short time after being set aside. After further development these animals have proved to belong to *C. s. strenuus.*
3. Dormant copepodids free of cysts have been seen among mud particles in a sampler with glass walls, immediately after being hauled up from the bottom. Upon examining the mud no traces of cysts were found.

From mud samples taken at all seasons in the tarn more than 3000 individuals were counted and studied. The results are shown in Table I.

Table I. *The distribution of the different stages present in the mud samples examined*

Nauplii	0
Copepodid I	0
Copepodid II	0
Copepodid III	2
Copepodid IV	3043
Copepodid V	20
Females	10
Males	3

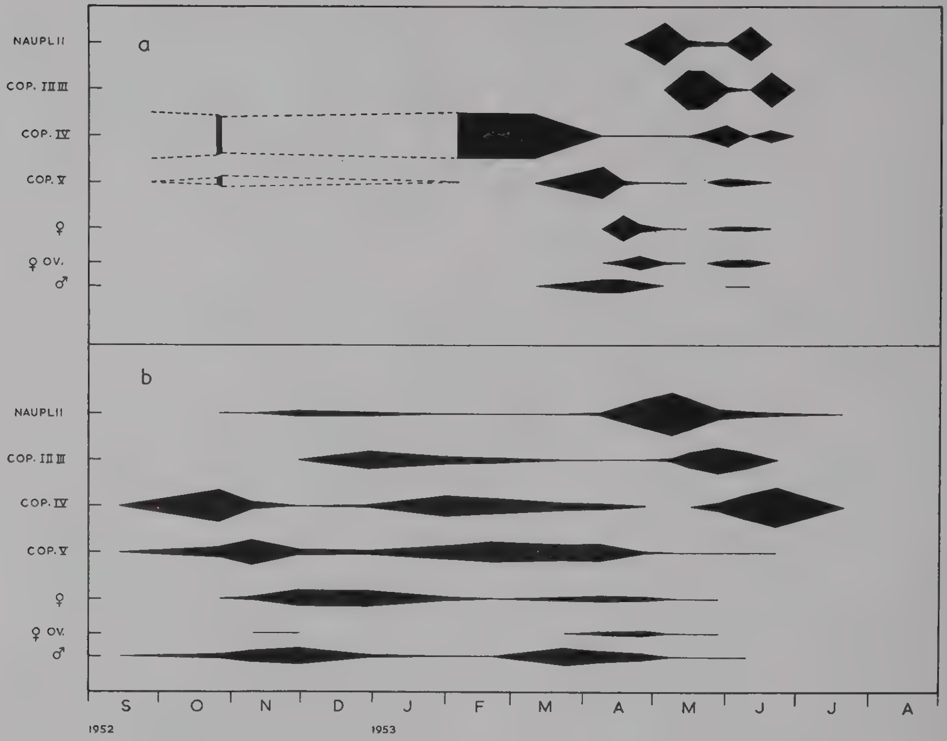

FIG. 1. Annual cycle in open water of two populations of *Cyclops strenuus strenuus* 1952-53. (a) in one of the ponds, (b) in the tarn. The different stages are given in per cent of total population. The curves are based on the counting of about 20,000 individuals.

The table shows that less than one percent of the animals belonged to copepodid stage V. Since these were uniformly distributed throughout the year, and since moulted stage IV skins were found, it is probable that the stage V copepodids developed after the samples were set aside for a period of about 30 hours. Even smaller numbers of other stages were found, which were presumably introduced by accident as they were found only at times when these stages were present in the water above. A large mud sample taken in summer, from which the animals were separated by filtering and killed at once, gave copepodids of the fourth stage only. Thus all results combine to show the fourth copepodid stage as physiologically peculiar in being capable of dormancy in *C. s. strenuus.*

In *C. bicuspidatus thomasi* the resting stage is also the fourth copepodid stage, while in *C. leuckarti* it is primarily copepodid stage V, although in the latter species a small proportion of stage IV animals were also found emerging from the mud samples (Fryer and Smyly 1954).

The stage-IV copepodids of *C. s. strenuus* that come directly from the mud are hyaline with a clear green tinge, and have conspicuous red droplets of oil in the body cavity. The gut, with very few exceptions, is empty. The resting animals are always very clean and mud particles are never found attached to them.

Dormant *C. s. strenuus* seem to be less deeply torpid than the other copepods with known resting stages. Fryer and Smyly (1954) give a minimum time for revival of about 4 hours for *C. leuckarti,* and considerably longer time is required for the encysted forms. *C. s. strenuus,* on the other hand, was seen to perform very slow and irregular swimming movements immediately after being hauled up from the bottom of the tarn. The movements were interrupted by long periods of immobility in which the animals were seen to sink down among mud particles in indifferent positions, often with the head or back down. When the mud sample was diluted with tap water many animals were found swimming normally in the

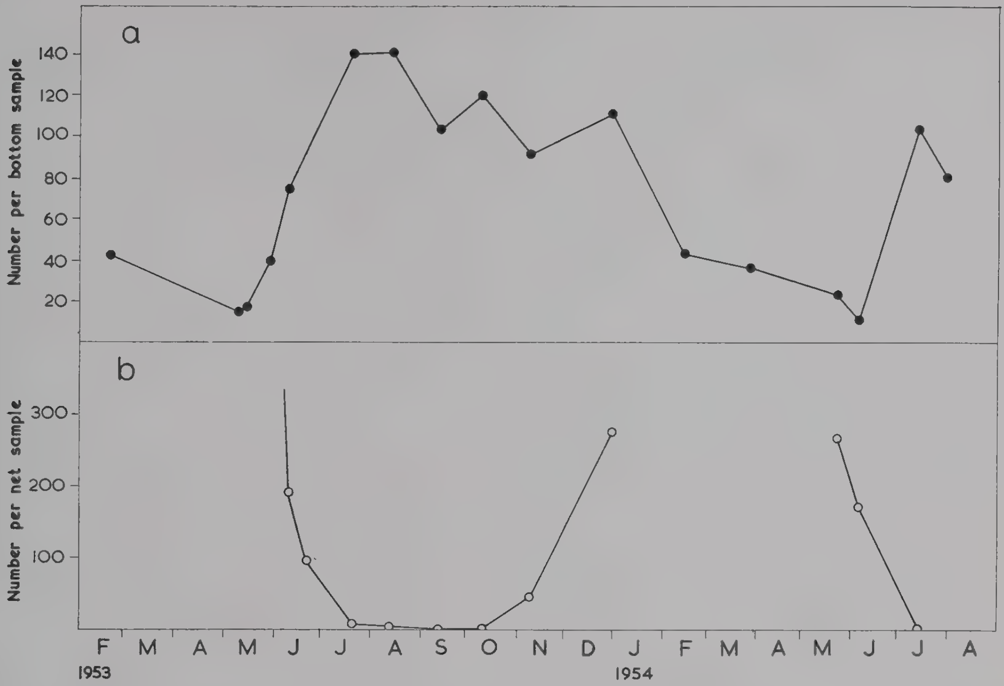

FIG. 2. Comparison of numbers of dormant (a) and free-swimming individuals (b) of the same generation in the tarn.

water above the mud as soon as the water had cleared sufficiently to allow them to be seen.

The maximum number of dormant individuals of *C. s. strenuus* found in the tarn was about 12,000 per square meter of bottom. This is far less than the maximum numbers recorded for *C. leuckarti* and *C. bisuspidatus thomasi* (1,000,000 and 1,300,000, respectively). The lower density of *C. s. strenuus* is to be expected when seen in relation to the smaller volume of the biotope, and since the animals themselves are larger than the other two species.

Dormant copepodids of *C. s. strenuus* are found in greatest number in summer, when the subspecies is absent from the open water. The variation throughout the year in numbers of resting copepodids in the mud of the tarn is shown in Figure 2a. The numbers vary reciprocally with the number of animals of the same generation living in the open water (Fig. 2b). In Figure 2a one sees that resting copepodids are found in the tarn at any time of the year also at times of optimum activity in the open water during spring.

The duration of the resting period has been found to vary greatly in different localities and from year to year in the same locality. Dormancy always starts in late spring or early summer and has been demonstrated to last from about 2 months to at least 10 months. In one of the ponds revival took place in 1951 as early as the end of August, and was followed by development of at least a part of the population. In the autumn of 1952 only occasional individuals of *C. s. strenuus* were found in daylight in the same pond, whereas many stage-IV copepodids and a small number of stage V were taken in the open water at night during October (cf. Fig. 1a). In the following year very few individuals were caught either in daytime or at night until April of the next spring. The fact that resting copepodids were found during the maximum of spring development in the tarn (Figs. 1b, 2a) makes it probable that the resting period may last more than 10 months, at least for a small part of the population. Because of overlapping of generations, however, no maximum time for the resting period can be established.

The great variation in the length of the resting period indicates a high degree of dependence upon environmental factors.

FACTORS REGULATING THE PERIOD OF DORMANCY

As to the nature of environmental factors regulating dormancy, some working hypotheses are set forth below, arrived at during investigations for a series of years in the localities mentioned. Observed facts make the assumption reasonable that revival from dormancy may be caused by sudden changes in external conditions, especially fluctuations in temperature and oxygen contents provided the temperature in the biotope is below approximately 10° C.

A very sudden fall in temperature caused by cold river water flowing into the ponds in the late summer 1951 caused a very marked revival, followed by further development at an unusual early time. In a series of years the autumnal revivals are found to be most frequent in the ponds having the greatest fluctuations in environmental factors. In the tarn the autumnal overturn is believed to be the initiating factor for the autumn revival, as in both 1952 and 1953 the overturn occurred directly prior to the emergence of the first copepodids from the bottom. The great majority of resting animals, however, became uninfluenced by the radical changes brought about by the autumnal overturn. The marked period of emergence during January 1954 (cf. Fig. 2a) is simultaneous with a change from aerobic to anaerobic conditions in the bottom layers of water.

The working hypothesis also explains the fact that the time of ice-melting in spring, with its marked changes in physical and chemical properties of the water, in the ponds is the time of revival and further development for nearly all individuals that have not hitherto emerged from the mud. But biotic factors also probably play a role in this complex problem, as do internal physiological changes that take place during the resting period.

The factors initiating dormancy in early summer are more obscure. The hypothesis of an escape from the warm water of summer seems reasonable for the ponds. In the tarn, however, layers of cold water with satisfactory oxygen tension are available all summer, though there is a rise in the mean temperature of all layers when dormancy is started.

Conditions in the ponds and in the tarn are very different when the resting period begins. In the shallow ponds the bottom layers of water are warm (15° to 20° C), are aerobic and exposed to light in the daytime, while in the tarn the bottom layers have a constant temperature of about 6° C, are anaerobic, and remain in darkness. The similar response to such different conditions suggests the probability of an internal timing mechanism. Observations in the ponds indicate, however, that a pause in development is not necessary in the life cycle of *C. s. strenuus*. This is shown by the fact that a population of stage-IV copepodids, newly produced in the spring, continued to develop in two of the ponds without an intervening resting period. In the same year, however, the population of stage-IV copepodids in other localities did not undergo this direct development, but descended to the bottom to become dormant.

These two types of vernal development are shown in Figure 1. In Figure 1 a stage-V copepodids and adults follow immediately after a maximum of stage-IV copepodids in the beginning of June, while no such development is found in the tarn (Fig. 1b). Direct development from stage IV was only found to take place in ponds that had been flooded with cold river water just before.

It is worth noting that the decrease in the numbers of *C. s. strenuus* in late spring runs counter to a general increase of other zooplankters, especially rotifers. This suggests a possible influence of external metabolites, or other biotic factors.

Comparisons with C. bicuspidatus thomasi

A comparison of the annual cycle of *C. bicuspidatus thomasi* as given by Birge & Juday (1908) and Cole (1953) with that of *C. s. strenuus* shows many striking features in common, and the problems posed by the resting stage are the same in both cases. Both copepods have their chief period of reproduction in the spring, and in the course of early summer they leave the open water, passing the summer in the bottom mud, often under anaerobic conditions, as resting stage-IV copepodids. Both may return to the open water in autumn, but in both the revival can be delayed up to at least 10 months, depending on environmental circumstances. Chief ecological differences between the two subspecies seem, at the present stage of knowledge, to be that *C. s. strenuus* lacks cysts and that *C. bicuspidatus thomasi* lives in large lakes where *C. s. strenuus* is not found. *C. biscuspidatus thomasi* has also been found in a shallow pond, the usual habitat of *C. s. strenuus*.

A detailed study of the phenology of these forms would yield further material for the comparison of the ecology of these two systematically and geographically separate copepods. As *C. bicuspidatus thomasi* seems to be confined to the nearctic region whereas *C. s. strenuus* is palaearctic so far as is known, the two subspecies may be said to be vicariating forms in phenological respect.

Studies in the annual cycle of *C. s. strenuus* in relation to environmental factors are being continued and a more comprehensive account will be published elsewhere.

SUMMARY

A resting stage without encystment has been found in *Cyclops strenuus strenuus* Fischer from localities in southern Norway, the stage of dormancy being the IVth copepodid stage. The resting period is primarily confined to the summer season, but dormancy may regularly be prolonged for at least 10 months. Environmental factors probably play an important part in the regulation of the resting period. Rapid changes in physical and chemical factors combined with low temperatures are likely to be factors that may initiate revival from dormancy.

Except for the lack of a recognizable cyst the annual cycle of *C. s. strenuus* shows a striking similarity to that of the American *Cyclops biscuspidatus thomasi* Forbes.

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SOME EFFECTS OF METEOROLOGICAL FACTORS ON ALL STAGES OF *APHYTIS LINGNANENSIS*,[1] A PARASITE OF THE CALIFORNIA RED SCALE[2, 3]

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INTRODUCTION

As times passes it becomes more evident in biological control work that density-independent (usually abiotic) factors may indirectly play as important a role in successful control as density-dependent (usually biotic) factors. True, in areas more or less optimum for a given pest, only biotic factors may act in such a manner as to bring about control at a low average population density; however, abiotic factors in these areas may not be optimum so far as the natural enemies are concerned, and, hence, control of the pest may be neutralized. Most of the work describing population interactions between hosts and natural enemies developed by biomathematicians has ignored abiotic variations in the environment. It is obvious to the field entomologist that in many, if not most, cases such variation is at times extreme enough to effect seriously either the pest, the natural enemies, or both. When such variations occur at regular intervals (for instance as winters do), then otherwise efficient natural enemies may not be left with an uninterrupted period of sufficient length within which to obtain and maintain control of their host. Clausen (1952) in one of the first general discussions of this problem states, "In temperate regions, enforced hibernation during the winter often brings several complications

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[1] This newly described species, formerly known as *Aphytis* "A", was imported from China and Formosa. Specimens are on file in the collection of the Department of Biological Control, University of California, Riverside. *Aphytis chrysomphali* (Mercet), a closely related species long established in southern California, made up a small proportion of the field counts. In general, the conclusions made herein with respect to *A. lingnanensis* apply to *A. chrysomphali* as well.

[2] Paper No. 860, University of California Citrus Experiment Station, Riverside, California.

[3] The authors gratefully acknowledge the assistance and advice of other members of the staff of the Department of Biological Control. C. A. Fleschner and E. J. Dietrick contributed materially to the early phases of this work. Joe Caprio, Experiment Station Statistician, was responsible for statistical analyses. Ken Arakawa and Harry Maltby assisted during the later stages of the field work.

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that may entirely prevent establishment and effectiveness. The introduced species may not be able to withstand the low temperatures, though these are not detrimental to the host. . . . We must consequently recognize, in biological control work, that any pronounced departures in climatic conditions from one which is constantly favorable throughout the year in temperature, rainfall, and humidity is certain to reduce the frequency of success."

The present paper deals with evidence acquired over a six-year period on a parasite which intrinsically is capable of controlling its host at low population levels but in certain areas is prevented from doing so by adverse weather conditions, principally low winter temperatures. Remarkably similar results, differing only in degree, have recently been reported by Lord and MacPhee (1953) in an excllent paper dealing with the ecology of *Lepidosaphes ulmi* (L.) and its parasite *Aphytis mytilaspidis* (LeB.). They showed that natural control of the oyster-shell scale by *Aphytis mytilaspidis* usually occurs in the mild-wintered Annapolis Valley of Nova Scotia but that the severe winters (−20°F. or lower) of central New Brunswick limit the success of the parasite.

In a paper concerning developments toward biological control of the California red scale, *Aonidiella aurantii* (Mask.), by *Aphytis chrysomphali* and *Aphytis* "A," DeBach *et al.* (1950) stated that "there are indications that the California red scale in certain areas . . . may not be so amenable to natural control by *Aphytis* as elsewhere." Additional information gathered up to 1954 emphasized the truth of this statement and has permitted, in part at least, analysis of the factors responsible.

From the field data acquired, it has been consistenty evident that *Aphytis* populations in certain areas of southern California are depleted out of all proportion to the California red-scale population during the winter and in some areas at other times of the year. Laboratory studies have shown that low temperatures are the principal cause of mortality. During the remainder of the year in southern California, *Aphytis* populations tend to increase although high temperature-low humidity-induced mortality may occur in summer and fall.

Southern California topography is exceedingly varied and this results in a diversity of environmental conditions within short distances. Mountains and hills serve as barriers to the movement of air currents coming from the ocean as well as from the desert. Areas which are cut off from the coast tend to be hotter in summer and colder in winter than those along the coast. Figure 1, which shows mountain barrier areas in black, illustrates how climatic zones in the citrus areas are affected by such barriers as well as by their distance from the ocean. The zones indicated in Figure 1 are approximate, but they furnish a fair idea of the citrus areas mentioned in this paper by the designations of coastal, intermediate, or interior. Within each of these zones small local areas may have a microclimate characteristic of one of the other zones.

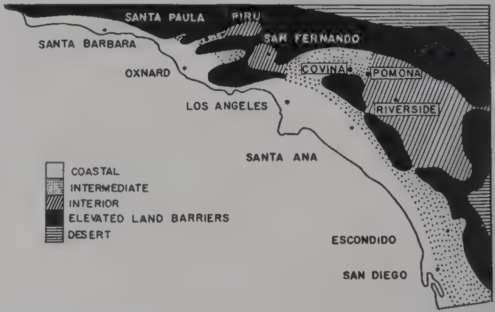

Fig. 1. General climatic zones in southern California citrus areas.

Field Studies

"[*Many insects*] *accustomed to warm surroundings. . . . soon die even at temperatures well above freezing-point. The cause of death is not understood. It is often attributed to the accumulation of toxic products which at normal temperatures would be eliminated. . . . This type of effect by cold is sometimes termed the 'quantity factor' because it must act for some time before it causes death.*"—Wigglesworth, 1939, p. 364.

In the early spring of 1949 field observations and counts showed that a high proportion of *Aphytis* pupae were dead. Since that time detailed semi-monthly or monthly counts on live and dead pupae have been made at various stations in southern California. Inasmuch as pupal counts are the most accurate for field-collected material, they, exclusively, will be used in this paper for purposes of presentation. All stages, however, are affected adversely, as will be shown later by laboratory data. These data were all derived from population samples made in completely untreated citrus groves, so effects from insecticides were never involved. *A. lingnanensis* was colonized in large numbers in all test plots and usually became dominant over the original *A. chrysomphali* populations within one year. However, *A. chrysomphali* constitutes a small proportion of the field counts. Counts were made by bringing in California red-scale-infested citrus fruits from the field, dissecting under the stereoscopic binocular microscope, and recording live and dead stages of *Aphytis* as well as of the scales.

Differences in mortality between areas. Inasmuch as previous studies on natural control of California red scale by *A. lingnanensis* and *chrysomphali* have indicated that these parasites are more successful in coastal areas than in interior areas, a comparison of the relative pupal mortality in representative groves for the two areas has been made. These data are presented in Table I and represent monthly averages acquired during a four-year period.

TABLE I. *Average per cent dead* Aphytis *pupae per month for the period 1950-1953 in a coastal and two interior area groves*

	Grove location		
	1. Coastal: warmest winter, mildest summer. Santa Barbara	2. Interior: warm winter, severest summer. Riverside	3. Interior: cooler winter, mild summer. Claremont
January	14	40	25
February	22	52	61
March	56	51	80
April	44	46	84
May	27	27	62
June	28	42	68
July	15	47	26
August	21	24	15
September	24	44	26
October	25	18	14
November	34	27	20
December	31	42	25

It is evident from Table I that pupal mortality was considerably greater at the interior stations than at the coastal station, especially from January to June. This winter mortality will be discussed first, followed by a section on differences during the remainder of the year. Weather data were compiled from the records of the Santa Barbara Botanical Garden (coastal area No. 1), the University of California Citrus Experiment Station at Riverside (interior area No. 2), and from the United States Weather Bureau at Pomona for the Claremont region (interior area No. 3).

Winter mortality. An average of 80 per cent or more dead pupae was obtained during the months of March and April at the interior station (No. 3) having the most severe winter climate, whereas the only mortality at the coastal station (No. 1) above 50 per cent was in March when 56 per cent was recorded. The warmer interior station (No. 2), which is in a so-called frostless area, was intermediate. In general, the per cent dead pupae peaked for the year during March and April and then decreased. There seemed to be a tendency for pupal mortality to increase slightly from May to June, but no logical reason for this is apparent. The weather at that time of year should be close to optimum.

It might appear from the data in Table I that the most severe conditions occur in March or April because recorded mortality was the greatest in these months. Usually, however, January and February are the most severe winter months in southern California, and it is assumed that March and April mortalities reflect, in large part, previous adverse conditions which had a cumulative effect through eggs, larvae, and pupae. Other data, not herein reported, indicate that the observed increases in mortality are not due merely to accumulations of dead pupae. Successive counts usually show no indication that scales dead or parasitized the previous month remain on the tree to the extent of appreciably influencing the next count. Preliminary data now available indicate that *Aphytis* eggs subjected to sub-lethal low temperatures, then moved to optimum temperatures, may hatch and develop to the pupal stage only to succumb before emergence. Should occasional adverse periods occur in the field which are sublethal, it is evident that the cumulative effect could very well result in the type of mortality data presented in Table I. Particularly would this be true when it is realized that winter slows development, and that eggs deposited during January, assuming all lived, would not be expected to develop to adults until sometime in March. Thus, sub-lethal adverse temperatures acting against *Aphytis* eggs in January and February and against *Aphytis* larvae in February or March could very well produce cumulative effects resulting in peak pupal mortalities during March and April. Definitely lethal conditions could, of course, occur at any given time during the winter and cause considerable mortality to all stages at that time.

Differences in winter mortality between years. Since data from several groves are available for several successive years, it has been possible to analyze for differences in pupal mortality between years. For this purpose average monthly mortalities were derived for the same three groves for the winters of 1951-1952 and 1952-1953. These two winters represent, respectively, the most severe and the least severe, as far as pupal mortality is concerned, of the four winters for which detailed data are available. The data, which are graphed in Figure 2, show very striking differences in mortality between the two winters. Mortalities were similar in November, but by April of the 1951-1952 winter there was a peak of 97 per cent pupal mortality whereas only 45 per cent mortality was attained at the peak of the 1952-1953 winter. The most interesting and significant fact about these data is that the winter of 1951-1952, which resulted in extremely high pupal mortalities, was not an unusually severe freeze winter from the standpoint of its effect on citrus. This fact has caused considerable difficulty in analysis of the specific winter factors involved in *Aphytis* pupal mortality since the most obvious lead, extreme low temperatures, was not enough to explain the high mortality during this particular winter. The following discussion seeks to clarify this situation.

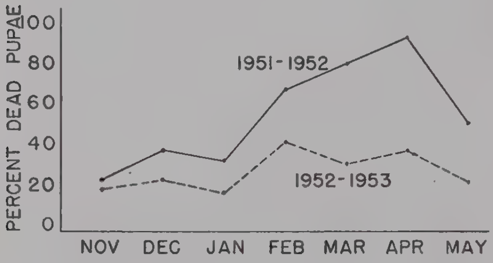

FIG. 2. Winter mortality of *Aphytis* pupae in different years.

Winter climatic factors and mortality. Several meteorological factors can be postulated as possible causes of winter mortality of *Aphytis* because of their departure from magnitudes expressed in other seasons. Average temperatures, evaporation and sunlight duration and intensity are lower, and rainfall is higher during winter months in southern California. Effects from all but temperature can be minimized for the following reasons. A lower rate of evaporation is known from laboratory studies to be beneficial, so except for occasional "north wind" periods, winter humidities are favorable. North winds create very dry conditions for from one to three days which may have an appreciable effect on adult *Aphytis,* without apparent damage to immature stages. Reduced sunlight duration and intensity should have no detrimental effect since the immature stages of *Aphytis* develop well in the laboratory in the virtual absence of light. Increased rainfall is probably not a factor because (1) rainfall is usually greater in coastal areas where it has been shown that mortality is less, and (2) one of the groves under study was irrigated by overhead sprinklers approximately once each week during the summer season, which corresponded with the period of lowest mortality. This leaves low winter temperature as the major possibility. In general, low winter temperatures give a fair correlation with observed *Aphytis* mortality. The data in Table II taken in three groves for a total of ten winter observations represent mean monthly minimum temperatures for December through March and an average of monthly per cent dead *Aphytis* pupae for the period of January through April.

TABLE II. *Mean monthly minimum winter temperatures and per cent dead* Aphytis

Grove location	Winter*	Mean monthly min. temp. °F. December through March	Average monthly per cent dead pupae Jan. through April
No. 1 Coastal: mild location. Santa Barbara	1949-1950	44.8	37
	1950-1951	46.4	36
	1952-1953	45.8	20
No. 2 Interior: fairly mild location. Riverside	1949-1950	45.0	44
	1950-1951	46.2	36
	1951-1952	46.0	69
	1952-1953	47.2	29
No. 3 Interior: colder location. Claremont	1950-1951	44.6	63
	1951-1952	41.4	70
	1952-1953	43.2	56

*Insufficient mortality data were obtained for No. 1, 1951-1952 and No. 3, 1949-1905.

These averages show a negative correlation between mean monthly minimum temperatures and per cent dead *Aphytis* pupae of 0.6358. This would indicate that minimum temperatures alone do not tell the whole story.

The poorest fit among these observations was for the winter of 1951-1952 in grove No. 2 where a rather high mean monthly minimum (*i.e.,* warmer than average) of 46.0°F. was associated with a high monthly average of 69 per cent dead *Aphytis* pupae. These figures were thought to be substantially accurate, and, finally, at least a partial explanation for the deviation was found. The winter months (December through March) of 1951-1952 had an appreciably lower mean monthly maximum temperature than the three other winters studied, especially in the area of grove No. 2 where the greatest deviation occurred. In this area the mean monthly maximum temperatures were from 4.4 to 6.5°F. lower for 1951-1952 than for 1949-1950, 1950-1951, or 1952-1953. It would appear likely, therefore, that an interaction between low temperatures and high temperatures during winter results in the observed mortalities. Regarding this point Harries and Douglass (1948) in their fine ecological work with *Eutettix tenellus* (Baker) state, "The effect of cold periods during the winter . . . appears to depend to an important extent on the daily maximum temperatures, since the intensity of subfreezing temperatures . . . have little effect when relaxed by the diurnal temperature fluctuations." With this in mind, plus the laboratory knowledge that the developmental zero of *Aphytis* is around 60°F., and with the assumption that appreciable mortality results only below 50°F., several summations were made involving both high and low winter temperatures. The simplest of these was based on daily maximum-minimum temperatures. For each day the number of degrees above 60°F. was recorded in a plus column and the number of degrees below 50°F. in a minus column. These columns can be summed for any given period, and the difference between plus and minus will indicate the relative severity of that period. When this was done for grove No. 2 and compared with the data of Table II, the following was forthcoming:

Winter	Mean monthly min. temp. °F. December through March	Aver. monthly percent dead pupae January through April	Difference between summation of degrees above 60 °F. and below 50 °F. December through March
1949-1950..	45.0	44	+202
1950-1951..	46.2	36	+668
1951-1952..	46.0	69	−149
1952-1953..	47.2	29	+724

It will be recalled that the mean monthly minimum temperatures for the 1951-1952 winter failed to explain the high average mortality of 69 per cent which occurred. It appears clear from column 4, above, that a consideration of high temperatures helps considerably. The severity of the winter based on mortality (column 3) is in close agreement with the severity of the winter as determined by summation of high and low temperatures (column 4). Apparently the time above 60°F. is as important to *Aphytis* survival as time below 50°F. is to mortality. This is a much too simple method, however, when used as described, because critical causes of mortality may be masked. For instance, three severe weeks in a row are undoubtedly much more harmful to *Aphytis* than three equally severe weeks scattered through the winter between favorable periods. Also, this method does not give as good an agreement between the three groves of Table II as did the minimum temperatures only. These studies are being pursued in an attempt to develop a method for precise evaluation of average differences between areas as well as of relative severity of winters as they occur.

Summer and fall mortality. Reference to Table I for the data from July to December shows that there is much less difference in pupal mortality between areas during summer and fall. The coastal area grove No. 1 and the interior area grove No. 3 (which has a cooler summer than No. 2) averaged the least mortality and were very similar in observed mortality. This may be accounted for by the fact that although grove No. 3 is in a hotter, drier area than grove No. 1, grove No. 3 is irrigated by overhead sprinklers about once per week during the hot part of the year, and the ground is covered by a heavy mulch which remains moist constantly and probably tends to modify the grove climate considerably. Grove No. 2 is in the hottest part of the interior citrus area; it is isolated from other groves, and the trees are small so there is little modification of general summer climatic conditions. This is reflected by greater average mortalities during the hot dry months from July to September. In all areas mortalities from October through December are generally the lowest of the year, and differences in pupal mortality, if any, among areas are slight.

LABORATORY STUDIES

The field data preceding, using pupal mortality as an index, serve to indicate areas in southern California and periods of the year most adverse to *Aphytis lingnanensis* and *chrysomphali.* These data leave much to be explained; hence, laboratory information was acquired regarding the effect of temperature and humidity on all stages of *A. lingnanensis.*

Laboratory test units consisted of small tightly sealed battery jars which contained various concentrations of H_2SO_4 as the humidity controlling agent. Constant temperatures were achieved by placing the test units in well-regulated constant temperature cabinets. The host for *Aphytis* in all tests was the California red scale cultured on mature green lemons taken from one grove. For purposes of reducing moisture loss from the fruit, as well as delimiting the area of infestation, approximately 70 per cent of the surfaces of the lemons was covered with paraffin wax.

Constant low temperatures and mortality.

Tests were run at temperatures of 30°, 40°, 50°, and 60°F. constant for periods of ½, 1, 2, 4, and 8 days, using eggs, larvae, pupae, and adults of *Aphytis*. Relative humidity was held constant at 60 per cent. Each stage was exposed only during that stage alone for the time indicated and then held under optimum conditions (approximately 80°F. and 60 per cent R.H.) until sufficient time had elapsed for complete development or death to occur. Partial results from these tests are condensed into Table III, using only the 30°F. temperature in order to afford a simpler illustration of the relative mortality in time and between different developmental stages. Nine hundred and forty-one individuals were used in the 30°F. test.

TABLE III. *Per cent mortality* of different stages of* Aphytis *subjected to 30°F. constant and 60 per cent R.H. for various times*

Duration of exposure time:	Per cent dead			
Days	Eggs	Larvae	Pupae	Adults
1..............	41	82	10	100
2..............	83	100	Insufficient data	100
4..............	100	100	66	100
8..............	100	100	No data	100

*The mortality count of immature stages was made after removal of organisms from test conditions to 80 °F. and 60% R. H. and allowing sufficient time for development to the next stage. Direct mortality of adults was determined at intervals of 1, 2, 4, and 8 days after subjection to the test conditions. Virtually all individuals of a given stage develop to the next stage when held at 80 °F. and 60% R. H.

From these data it is evident that the adult stage was most susceptible to low temperatures, the pupal stage was least susceptible, and the egg and larval stages were intermediate. Larvae appeared to be somewhat more susceptible than eggs at 30°F.; however, additional data indicate that eggs may be more susceptible than larvae at somewhat higher temperatures (50° to 60°F.) with long (8 day) exposure periods. Table III does not emphasize enough the sensitivity of adult *Aphytis* to low temperatures; actually 90 per cent died after a ½-day exposure to 30°F. As would be expected, mortality increased with time of exposure, so that after four days at 30°F. all stages, except pupae, showed complete mortality.

In order to make a better illustration of the relationship between various temperatures, times of exposure, and mortality, the complete data acquired for the egg stage are given in Table IV. Fifteen hundred and forty-six eggs were used in this test.

TABLE IV. *Relation of various times of exposure and constant temperatures to mortality* of eggs of* Aphytis

Duration of exposure time:	Temp. °F.			
Days	30	40	50	60
½..............	0	0	0	0
1..............	41	6	0	1
2..............	83	5	8	2
4..............	100	10	5	3
8..............	100	100	40	23

*The mortality count was made after removal of eggs from test conditions to 80° F. and 60% R. H. and allowance of sufficient time for development to the larval stage. Virtually all eggs develop to larvae when held at 80° F. and 60% R. H. constant.

From these data one can approximate through interpolation the effect on egg mortality of any combination of constant temperature between 30° and 60°F. and exposure time of from ½ to 8 days. At 30°F. mortality increases rapidly with exposure times above ½ day, reaching 83 per cent dead at 2 days and 100 per cent dead at 4 days. Obviously there is a vast difference between exposure to 30°F. and 40°F. except for the longest period of 8 days. Four days of exposure to 40°F. resulted in only 10 per cent mortality. On the other hand, 8 days of exposure to the rather mild, low temperatures of 50° and 60°F. caused substantial mortalities of 40 and 23 per cent, respectively. Such exposures are not extremely unusual in southern California citrus areas; hence, it is evident that considerable mortality may result from prolonged cool spells without the necessity of freezing temperatures occurring.

Constant low temperatures and the rate of development. The foregoing tests furnished additional data which indicate that not only does mortality of immature stages result from exposure to low temperatures but that survivors when returned to optimum conditions do not develop so rapidly as would normally be expected. The following example of this "carry-over" effect, derived from exposure of eggs to low temperatures, illustrates this point. *Aphytis* eggs were subjected to various low temperatures of from 30°F. to 60°F. for 2 days and then removed to optimum conditions (80°F.) and held for 10 days. At the end of this holding period all should have been in the pupal stage; however, various retarded stages of development were exhibited. An average per cent of expected development was calculated from these figures based on known rates of development of normal individuals not previously subjected to low temperatures. The results are as follows:

Exposure temp. °F. (2-day period)	Per cent of expected development completed at 80 °F. 10 days after exposure
30	50
40	75
50	87
60	88

The significance of these data lies in the fact that immature stages may be slowed not only in development during actual exposure to cold but subsequent to it even though conditions following such exposure are optimum for growth. Under winter conditions, therefore, the chances of enough eventual exposure to cause mortality are greatly increased.

This brings out a point which needs emphasis. All the laboratory data heretofore recorded apply to exposure to low temperatures during one stage only in the development of the individual. In the field, of course, this does not usually happen in winter time. From December through March most, if not all, developmental stages of an individual *Aphytis* will be subjected to low temperatures. It is evident, therefore, that field mortality can easily be much greater for any given temperature than would be indicated from laboratory studies concerning exposure during one stage only. Certain earlier laboratory tests further demonstrate this point. Each immature stage of *Aphytis* was subjected constantly to 57°F. from that stage on until a pre-emergence pupal count was made of survivors that developed that far. Those which died before becoming mature pupae were not considered in this analysis. Of those which began as eggs, 98 per cent died as mature pupae. Those which began as young larvae showed 70 per cent mortality as mature pupae, and those which began as mature larvae or young pupae showed 62 and 60 per cent mortality, respectively, as mature pupae. In addition, as already mentioned, preliminary field data now being accumulated indicate that there may be a real cumulative effect from cold exposure, in that eggs subjected to low temperatures may develop normally, but more slowly, to the pupal stage only to succumb during emergence of the adult. Most laboratory data tabulated herein were based upon counts of mature pupae; hence, this possible additional mortality was not obtained.

During the final preparation of this paper, the first indication of a third and probably very important effect of low temperatures on *Aphytis* was discovered. In addition to causing mortality and producing "carry-over" effects on the rate of development, low temperatures also sterilize adult *Aphytis*. When a group of mated female *Aphytis* was subjected to 30°F. for six hours and the survivors (about 50 per cent) allowed to oviposit, the progeny were virtually all males (1779 males; 1 female), whereas normally about 80 to 90 per cent females are produced in the insectary using the same host. This means that the sperm in the spermathecae of the mated females were nearly all killed by subjection to 30°F. for 6 hours. A test involving 25 males which were subjected to 30°F. for 6 hours and then mated to 24- to 36-hour old virgin females, reared at a constant 80°, yielded 97 per cent male offspring. The obvious interpretation is that the males were likewise rendered sterile by this exposure, since production of female progeny in *A. lingnanensis* is nearly always contingent upon fertilization. Other sterility effects which operate through immature stages may occur. Such effects are discussed by Flanders (1938) and DeBach (1943). From the standpoint of adverse effects on natural control, sterility of *Aphytis* adults resulting from subjection to 30°F. for 6 hours assumes great importance, because such exposures occur rather commonly during the winter in southern California. Obviously if such exposures result in the production of practically all male progeny, populations of *Aphytis* would decline rapidly.

Alternating temperatures and mortality. Thus far it has appeared from the laboratory data that low temperatures (30° to 50°F.) are always detrimental to *Aphytis,* the ultimate effect depending only upon duration and intensity. It may be recalled from the discussion of the field data, however, that periods of high temperatures following low temperatures appeared to alleviate the adverse effects. Accordingly, laboratory tests were run to explore this hypothesis.

A constant relative humidity of 60 per cent was used in all tests. For these tests host material containing newly laid eggs of *Aphytis* was placed in a constant temperature of 40°F. for 12 hours, then removed to a constant temperature of 80°F. for 12 hours, then repeated until the life cycle was completed. Three hundred and five individuals were used in this test. Oddly enough, as it might seem, all but 7 per cent of the original eggs completed development to the adult stage. At least 3 per cent mortality during the complete life cycle is expected under optimum conditions; hence, very little mortality occurred. The developmental period was slightly more than doubled as would be expected, but the actual time spent at 80°F. (16.5 days) was only slightly more than in the checks. Checks run at 80°F. constant showed complete development from egg to adult in 15 days.

The most striking part about these results was that individuals could be subjected to an average total of 16.5 days at 40°F. during their life cycle and still develop through to adulthood. It will be recalled from Table IV that eggs subjected to 40°F. constant were all dead by 8 days. In fact eggs do not hatch up to 55°F. constant, and at 60° constant other tests indicate little development past young larvae. Those few which survived had an average life cycle of 54 days. This latter temperature (60°F. constant) gives the same average as the 40°F. for 12 hours, alternating with 80°F. for 12 hours, yet the life cycle is much longer at the constant cool temperature. Survival was also lower. Obviously, therefore, high temperatures following short exposures to low temperatures greatly reduce, and perhaps even neutralize, the adverse effects from low temperatures which would otherwise occur. It appears that the alleviating effect of the high temperatures must depend upon the length of time previously exposed to low temperatures, for it is highly probable that 40°F. for 12 hours, followed by 80°F. for 12 hours, will be less severe than 40°F. for 24 hours followed by 80°F. for 24 hours.

Table V. *Effects of different combinations of constant humidity and temperature on adult* Aphytis *as measured by time in days to 50 per cent mortality*

Temp. °F.	Relative humidity—per cent 20%	 50%	 80%
	Days to 50 per cent mortality		
50	3	7	9
60	5	11	22
70	7	11	18
80	2	6	7
90	1	4	7
Average	3.6	7.8	12.6

Effect of Humidity and Temperature Interaction on Mortality

The previous discussions concerning the effects of low temperature on *Aphytis* purposely have neglected humidity effects because low temperatures occur in southern California during that part of the year exhibiting the highest relative humidities, which are those most favorable to *Aphytis*. In addition, we have been dealing principally with immature stages of *Aphytis*, which under the protective scale covering of their host usually are in a highly humid microenvironment. Adult *Aphytis*, however, are more likely to be influenced by adverse humidity conditions.

Tests on adult *Aphytis* were conducted at three relative humidities, low (20 per cent R.H.), medium (50 per cent R.H.), and high (80 per cent R.H.) and at five temperatures ranging from 50° to 90°F. Results are presented in Table V. Nine hundred individuals were used in this test.

From these data it is clear that *Aphytis* adults are very seriously affected by low humidities. At 20 per cent R.H. they live on the average less than one-third as long as at 80 per cent R.H. The extreme effect, however, is seen at the high temperatures combined with low humidity. At 80° and 90°F. and 20 per cent R.H., adult *Aphytis* lived only one-tenth to one-twentieth as long as at 60° to 70°F. and 80 per cent R.H. It is also evident from Table V that adult longevity is adversely affected by high temperatures (*i.e.*, above 70°F.) regardless of humidity. It is known, also, that immature stages show considerable mortality at 90°F. and that they show some increase in mortality at low humidities. These data then help explain the higher pupal mortality observed in grove No. 2 (Table I) during the hot dry months of July and September.

During the period from about October to March, strong north winds of from one to three days' duration occasionally blow from the Mojave Desert through mountain passes and into the southern California citrus areas. During these winds, which are most severe in the interior valley citrus areas, the temperature is usually well above normal for that period of the year, and the relative humidity may remain below 10 per cent for 24 hours or more and below 20 per cent for 48 hours or more. Such conditions would approach those in Table V where at 20 per cent R.H. and 80° or 90°F. *Aphytis* adults lived only 1 or 2 days. Counts of adult parasites made before and after a strong "north" wind showed little reduction after 24 hours but nearly complete disappearance of the parasites after 3 days. The protected immature stages are probably not affected nearly so adversely as are the adults. These winds, then, have a considerable effect on *Aphytis* adults, much less on immature states, and relatively little on the California red scale, which is completely protected by the scale covering and has a constant supply of moisture from the plant as well. The effect of these winds will be to produce sharp oscillations in *Aphytis* populations but not steady declines.

Discussion

The preceding data have shown that considerable mortality to both immature and adult stages of *Aphytis* may result from the effect of various meteorological factors. Principal among these are low winter temperatures, high summer temperatures, and low humidities. The question may be asked, however, whether the observed mortalities actually seriously lower *Aphytis* populations to the extent that biological control is negated. Such a question is apropos inasmuch as many students of population dynamics have postulated that climate can have no controlling effect on animal populations. However, all the field evidence in the present case indicates that the various components of climate are the major factors keeping *A. lingnanensis* and *chrysomphali* from successfully controlling the California red scale in certain citrus areas. For instance, in the mild coastal climatic zone of southern California natural control of California red scale (control achieved without artificial periodic colonization of parasites) by *A. chrysomphali* or *lingnanensis* has occurred in every untreated citrus grove studied. In the less mild intermediate climatic zone, natural control of California red scale by *Aphytis* has occurred in certain groves and not in others, depending apparently upon microclimatic differences. In this intermediate zone, though, it has been possible to obtain biological control of the California red scale by yearly periodic colonizations of large numbers of *Aphytis* in all plots thus far studied. In the interior valley climatic zone, where extremes are greater, natural control rarely if ever occurs, and it has not been possible to achieve a consistent degree of successful biological control through the periodic colonization of parasites.

Parasite population density reflects the differences between climatic zones. A survey of 51 untreated groves in Los Angeles County in 1951 showed three times as many immature *Aphytis* per 100 scales in the intermediate climatic areas as in the interior climatic area of the San Fernando Valley. Actually, eradication of *Aphytis* nearly occurs following colder than normal winters in interior valley citrus areas. Often in such groves it is virtually impossible to find a live immature or adult *Aphytis* by March or April even though they were abundant the preceding fall.

Evidence that climatic factors may affect insect parasites and thus indirectly influence host populations has been given by Michelbacher and Leighly (1940) for field populations and by Burnett (1949) for experimental populations. Michelbacher and Leighly (p. 127-128) state, "Parasitism must be taken into account in any discussion of the climatic limitations of the alfalfa weevil. Climatic conditions favorable to the weevil may also be exceptionally favorable for one or more of its parasites. It is therefore conceivable that the weevil may be more destructive, or at least more abundant, in a climatic zone other than its optimum if the conditions in the zone in question are not optimum for maximum parasitism. . . .

"In California our observations have yielded evidence of such a phenomenon. When the weevil was first found in lowland middle California, it was most abundant at Pleasanton, Alameda County, and in adjacent areas near San Francisco Bay. The populations encountered in the infested part of the San Joaquin Valley were rather small in comparison with those found near the Bay. In 1933 and 1934 the United States Department of Agriculture Bureau of Entomology and Plant Quarantine introduced the larval parasite *Bathyplectes curculionis* (Thoms.), into the infested areas. The parasite readily became established and is evidently more effective about Pleasanton and in the Bay area in general than in the San Joaquin Valley.

"As a result of depredations of the parasite, the weevil populations now found in the Bay area are smaller than those found in northwestern San Joaquin Valley, a condition that is the reverse of that which was obtained before the parasite was introduced. . . . If the trends of the weevil populations were studied without any attention to parasitism, however, the conclusion might be reached that the climate of the northwestern part of the San Joaquin Valley is more favorable to the weevil than that of the areas close to San Francisco Bay, with their cooler summers and more moderate winters. Such is evidently not the case."

In southern California, parasitization has never been seriously considered previously as a factor which might help explain the differences in severity of the California red scale in various climatic zones. It is quite possible, however, that differences in difficulty of obtaining chemical control of red scale infestations may be explained in the same manner as was done by Michelbacher and Leighly (1940) for the alfalfa weevil. For instance, in Orange County, a coastal area, insecticidal control of the red scale is much easier than in Riverside County, an interior area. *Aphytis chrysomphali* is fairly common even in regularly treated citrus groves in Orange County, whereas these parasites are rare in Riverside County groves. Orange County groves have been observed which were sprayed for red scale control when, unbeknownst to the owner, ninety per cent of the scales were dead due to the acivity of *Aphytis*. It seems likely, therefore, that the parasites may be in large part responsible for the fact that red scale is not so difficult to control in

Orange County as in Riverside County. Usually these differences are explained by the fact that the number of generations per year of red scale is somewhat greater in interior areas; however, mortality because of summer and winter extremes is also greater, so that the net result, *if there were no parasites,* could be that red scale would be a worse problem in Orange County.

Burnett (1949) has shown with experimental populations of *Trialeurodes vaporariorum* (Westwood) and its parasite *Encarsia formosa* Gahan that different mean temperatures result in quite different population interactions between the host and parasite. At 18°C. the host population increased more rapidly than the parasite population; at 24°C. host and parasite rates of increase were about equal, whereas at 27°C. the parasite population increased more rapidly than that of the host so that it dominated the host. These results were due to a differential effect of temperature on the fecundity and rate of development of the host and parasite. Obviously such results could explain why natural control in the field occurs in certain years and not in others or in certain areas but not in others.

SUMMARY

Field data based upon a pupal mortality index show that *Aphytis* populations in southern California are more or less greatly reduced by low winter temperatures. The effect varies in different years and is relatively less in coastal (mild winter) areas than in interior valley (colder winter) areas. Close to 100 per cent pupal mortality has been recorded in interior areas; hence, natural control of California red scale usually occurs in untreated groves in coastal areas and rarely in such groves in interior areas. Subfreezing or average minimum temperatures are not necessarily the best index to mortality. Maximum temperatures (above 60°F.) have a favorable modifying effect, depending upon frequency and intensity. The *Aphytis* pupal mortality index also shows a decided increase during the hot dry months of July, August, and September in the more severe interior climatic areas.

Laboratory studies under controlled temperature and humidity conditions showed that all stages of *Aphytis* are adversely affected by low constant temperatures of from 30°F. to 50°F. and in some cases 60°F. depending upon duration of exposure. The adult stage was most susceptible, with 100 per cent mortality occurring after less than one day's exposure to 30°F. Cold-sterilization of sperm in the males and in the spermathecae of the females also occurs at low temperatures. The pupal stage was most resistant; however, four days of exposure at 30°F. caused 66 per cent mortality. Effects on the egg and larval stages were intermediate. Complete mortality occurred to each of these stages after 2 to 4 days' exposure to 30°F. Four to eight days' exposure to 40°F. or 50°F. caused considerable to complete mortality to these stages. Prolonged exposure of 8 days at 60°F. caused some mortality. Eggs do not hatch up to 55°F. constant, and little or no development past young larvae occurs at 60° constant. Exposure of eggs to low temperatures had a carry-over effect after removal to optimum conditions. Rate of development under optimum conditions was reduced in relation to intensity of previous exposure to low temperatures. Equal but short alternating periods of high (80°F. for 12 hours) and low (40°F. for 12 hours) temperatures nearly eliminated the expected adverse effects which the low temperatures alone would have shown.

Aphytis adults are seriously affected by low atmospheric humidities, while immature stages, because of their protective niches, are less affected. Life expectancy of adults at 20 per cent R.H. was less than one-third as long as at 80 per cent R.H. High temperatures combined with low humidities produced extreme effects; life expectancy at 90°F. and 20 per cent R.H. was only one-twentieth of that at 70°F. and 80 per cent R.H.

High temperatures (90°F) greatly reduced the life-expectancy of adult *Aphytis* regardless of humidity, and the same applies to immature stages. These data indicate that climatic zones in which an insect population is most abundant may not necessarily be the optimum zone. Biological control may occur in the zone optimum for the host; hence, the host will be scarce. Biological control may be neutralized by climatic factors in a zone suboptimum for the host; hence; the host will be relatively abundant. The net result will be a host most abundant in a suboptimum climatic zone.

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NOTES AND COMMENT

FALL DISTRIBUTION OF BIRDS IN A PALOUSE RIVER CANYON

During the fall and winter of 1953 the writers undertook a general ecological study of a portion of the Palouse River valley, near Armstrong, Whitman County, Washington. During the course of these investigations records were kept on the numbers of birds observed and the vegetation in which they were located. It was anticipated that these observations might indicate bird-use of the major vegetational types found in the area.

Several investigators (Dumas 1950; Wing 1949) have published distributional data for birds of the Palouse grassland during the nesting period, but few have been concerned with distribution patterns during the fall migration.

The writers wish to thank Dr. George J. Wallace for critically reading the manuscript.

Location and Vegetation

The area of study was located about one mile north of Armstrong, and included a representative section of the river canyon. This area measured approximately one-half by one mile, parallel to the river, and included the river bottom and the adjoining slopes. A variation of about 100 feet vertical distance was found between the river and the top of the canyon slope.

According to Daubenmire's classification (1942) the study area lay within the Festuca-Agropyron zone. However, local conditions were apparently drier than average, with the result that the area showed the aspect of the Agropyron-Poa zone, which is typical of conditions farther west. The Agropyron-Poa association was found on the upper slopes on both sides of the river canyon. Most of this vegetation exhibited extreme disturbance from overgrazing. The Agropyron-Poa association was bounded on the upper side of the valley slope by wheat and pea fields and on the lower side by thickets of *Crataegus douglasii*.

Crataegus occurred in erosion gullies on the canyon slopes and also was an important representative of the floodplain forest found on the valley floor. Other dominant trees of the floodplain forest included *Betula microphylla, Populus tremuloides, Populus trichocarpa,* and *Salix* spp. *Crataegus* and *Betula* commonly formed dense stands which almost completely excluded herbaceous undergrowth. In one large area *Populus tremuloides* was dominant over *Crataegus,* and excluded other woody species completely, with the exception of a few tall cottonwoods, *Populus trichocarpa.*

A moist meadow dominated by *Elymus cinereus* occurred on a level part of the valley floor. In the Elymus community *Rumex* spp., *Sisymbrium altissimum, Arctium minus, Dipsacus sylvestris,* and *Heracleum lanatum* were present. A few woody shrubs, mainly *Symphoricarpos albus* and *Rosa* spp., also occurred here.

Minor vegetational areas included a small marshy depression near the river. The very moist conditions allowed a dense growth of *Phalaria arundinacea* around the borders of the water. *Carex* spp. and *Poa* spp. made up the rest of the marsh vegetation. Other portions of the valley floor were cleared for pasture and wheat fields.

The importance of each vegetational type in the study area is shown in the following tabulation:

Vegetational Type	*Per Cent*
Floodplain forest	40
Agropyron-Poa	36
Elymus	3
Annual Weeds	1
Other	20
Total	100

Methods

Trips to the study area were made at weekly intervals from September 26 to December 19, 1953. Observations were made approximately an hour after sunrise. Routes included both in a longitudinal and transverse transect of the river canyon. One observational transect ran along both sides of the Palouse River and included plowed fields, the floodplain forest, the Elymus community, patches of annual weeds, and the small marsh. The second transect ran principally through the Agropyron-Poa association, and the floodplain forest. Notes were taken on all birds seen within the study area, recording the vegetational type or plant species each bird or group of birds was utilizing.

Results and Discussion

The relative value of each vegetational type to birds is presented in Table I. Occurrence indicates that a bird or group of birds was observed feeding, perching, or hiding in or under that particular vegetation. "Other" refers to plowed fields, pasture, or uncommon habitat not included in the table.

Since the floodplain forest covered almost one-half of the study area, it was expected that this vegetational type would be most important to birds. Birds observed here

Table I. *Occurrence of single birds or groups of birds in major vegetational types*

Species	Major Vegetational Type				
	Floodplain Forest	Agropyron-Poa	Elymus	Annual Weeds	Other
California quail	8	..	1	3	..
Ring-necked pheasant	14	4	4	5	3
W. mourning dove	2	..	..	..	..
Red-shafted flicker	12	..	..	..	..
American magpie	9	..	..	..	..
Black-capped chickadee	27	..	..	3	1
American robin	22	2	..	..	1
Ruby-crowned kinglet	4	..	..	1	..
Cedar waxwing	7	..	..	3	1
Western meadowlark	..	3	..	..	..
Evening grosbeak	2	..	..	..	..
Common redpoll	1	..	..	..	..
Pale goldfish	1	..	2	..	..
Spotted towhee	1	..	..	..	..
Oregon junco	20	1	1	4	5
White-crowned sparrow	3	..	..	3	..
Song sparrow	12	..	1	1	..
Total	145	10	9	23	11

TABLE II. *Occurrence of single birds or groups of birds in the floodplain forest*

Species	*Crataegus*	*Betula*	*Populus tremuloides*	*P. trichocarpa*
California quail	8	..	..	..
Ring-necked pheasant	12	1	1	..
W. mourning dove	2	..	..	..
Red-shafted flicker	8	..	..	4
American magpie	8	1	..	..
Black-capped chickadee	24	..	..	3
Western robin	13	..	1	8
Ruby-crowned kinglet	4	..	..	..
Cedar waxwing	5	..	1	1
Evening grosbeak	1	..	1	..
Common redpoll	..	1	..	..
Pale goldfinch	1	..	..	..
Spotted towhee	1	..	..	..
Oregon junco	20	..	..	..
White-crowned sparrow	3	..	..	..
Song sparrow	11	..	1	..
Total	121	3	5	16

were also generally thicket-dwelling species. Occurrence of birds in the dominant tree species of the floodplain forest is presented in Table II. It will be seen immediately that *Crataegus* was by far the most important part of the native vegetation for birds during the period of study. This was probably the result of the profuse fruit it produces as well as the excellent protection which its dense and thorny branches provide. Although cottonwood was a relatively rare tree on the area, it was used to a fairly large extent, particularly by robins and cedar waxwings which seemed to prefer the open view and height which it provided. Although the proportion of birch was nearly one-half that of *Crataegus*, it was almost completely ignored by birds.

Certain species, such as the western meadowlark, were restricted to one or two vegetational types. Other species, such as the Oregon junco, were seen almost everywhere. Despite this variation, it is evident that *Crataegus* assumed a position of importance which far exceeded its percentage composition of the total vegetation.

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PENETRATION OF ROOTS OF TALL WHEATGRASS IN WET SALINE-ALKALI SOIL

Tall wheatgrass, *Agropyron elongatum* (Host) Beauv., is gaining a reputation for ability to produce high yields of pasturage and to grow better than other grasses on wet saline or alkali soils. It is believed to be beneficial in the reclamation of tight alkali soils, once irrigation and drainage have been established.

Two locations were selected for root study in a 4-year-old 75-acre field of tall wheatgrass on the Nevada Nile Ranch, 4 miles south and 1 mile east of Lovelock, Nevada. This is the smallest of 11 fields of tall wheatgrass aggregating over 2,000 acres on this ranch.

The first location supported a full stand of tall wheatgrass with remnants of native inland saltgrass, *Distichlis stricta* (Torr.) Rydb. (Fig. 1.). The second location was one which had a poor stand of tall wheatgrass and no other vegetation, apparently because of greater salinity, alkalinity, and sodium content in the upper 2 feet of soil. (Fig. 2.)

Excavations were made by G. A. Momberg to the water table at 12 feet in the first location and to 10 feet in the second.

Soil samples were taken for chemical analyses at the surface, at 12 inches, and at the even foot depths to the water table. The analyses were performed by R. E. Eckert under the supervision of L. E. Dunn.

Except for the 12-foot level in the more favorable site for tall wheatgrass, all levels were 8.7 or above in pH, indicating a relatively high exchangeable sodium percentage and the presence of alkaline-earth carbonates, a condition commonly known as "black alkali."

A sample of water from the bottom of the first trench was found to contain sodium, 92% relative to all cations present. Total salt concentration expressed as electrical conductivity was 5,000 micromhos, or .35 per cent by weight. These data indicate that the water is not suitable for irrigation (Wilcox 1948).

After preliminary inspection, and establishment of the presence of grass roots at the bottoms of the trenches, an attempt was made to expose the roots by washing the tight clay walls of the trenches.

Although approximately 200 gallons of water under high pressure were sprayed on each profile, resulting exposure of severed root-ends was disappointing except in the fine sandy material at the 7 to 10 foot levels. The attempt raised the water level about 1 foot, and so interfered with the investigation of root distribution at the maximum depths.

A square-foot frame was used foot-by-foot down one face of each trench to facilitate charting the positions of the exposed root ends. The results of this charting and the soil analyses appear in Figure 3. Saltgrass rhizomes were present to a depth of 27 inches. Because of the presence of innumerable fine saltgrass roots, the roots in the top 30 inches of the first trench were not charted. Root samples of saltgrass from the first foot of soil were determined by R. H. Miller as being not of the same species as root samples from the 11-foot depth. Tall wheatgrass was the only other species present.

Roots were less numerous at comparable levels in the profile which was highest in per cent salt and sodium, and

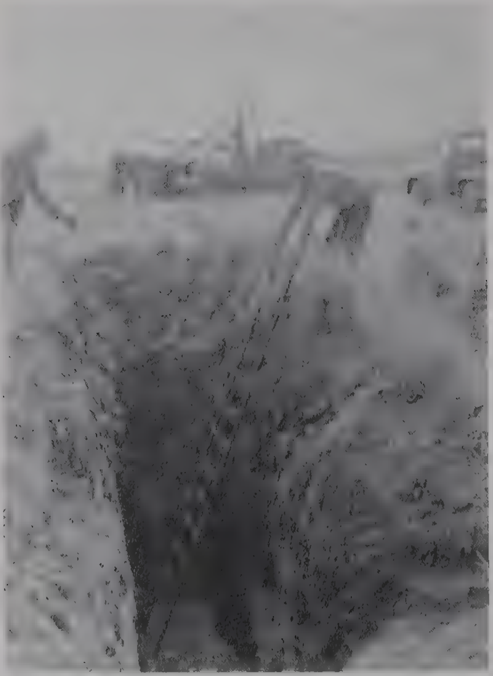


FIG. 1. Trench to 12 feet in a good stand of tall wheatgrass.

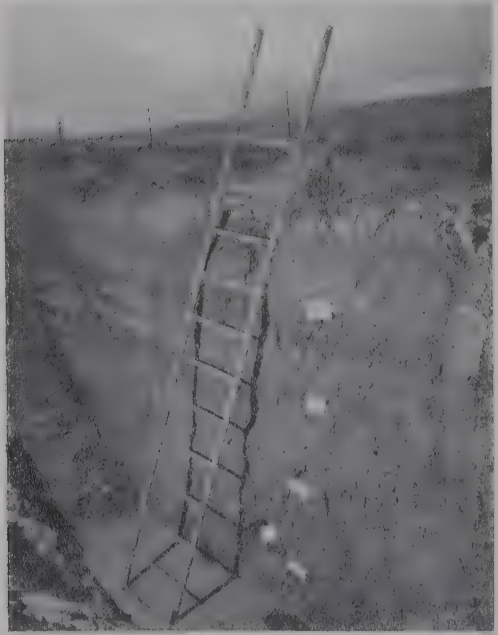
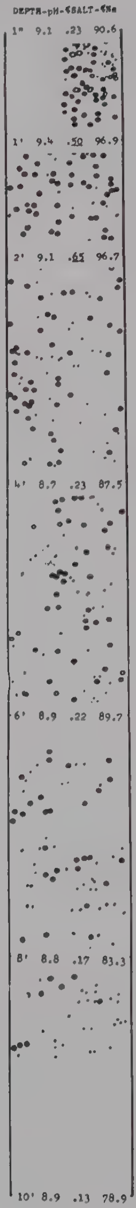
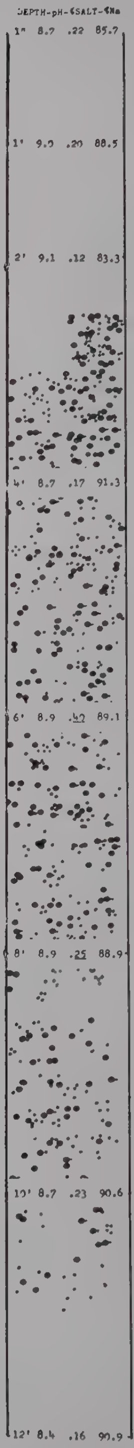


FIG. 2. Trench to 10 feet in the second location with higher alkalinity and a poor stand of tall wheatgrass.





in reaction. This was in close agreement with the differences in stands of grass on the two sites.

The observations reported in this paper add to previous information on salt and alkali tolerance of tall wheatgrass (Plummer, *et al.* 1955, Weintrab 1953). They also explain, in part, the ability of this grass to grow on semiarid non-irrigated, or occasionally irrigated, land.

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A NOTE ON THE PHYTOPLANKTON-ZOOPLANKTON RELATIONSHIPS IN TWO LAKES IN WASHINGTON[1]

The purpose of this note is to present some information on the quantitative relationships noted during the period March 1950 to March 1951 between phytoplankton and zooplankton in two saline lakes in Central Washington. It has been observed frequently that a tendency toward a low or inverse correlation exists between phytoplankton and zooplankton population density. Explanations of these observations have been advanced by Harvey *et al.* (1935) and Hardy and Gunther (1935). Harvey proposes that the grazing effect of the herbivorous zooplankton is sufficient to limit the phytoplankton population in time as well as in quantity. On the other hand, Hardy states, in his "hypothesis of animal exclusion," that the zooplankton avoid or are prevented from living within areas of dense phytoplankton, presumably due to unfavorable chemical conditions produced by the phytoplankton population. Hardy also maintains that the two factors, grazing by the animals and the excluding influence of the phytoplankton, are not antagonistic and may be in operation simultaneously. It is thus important to present data which clearly indicate inverse phytoplankton-zooplankton relations and to evaluate them in terms of the above described concepts.

The two lakes studied are the southernmost of a series of lakes in the lower Grand Coulee (Bretz 1932). Soap Lake, the terminal one in the series, has a maximum length of 3.6 km., an area of 336 ha. and a maximum depth of 26 m. The lake is meromictic, its monimolimnion occupying the bottom 7 meters of the basin. During the period of study the salinity of the mixolimnion was 35 gm. per liter of total dissolved salts whereas that of the monimolimnion was approximately four times that of the upper waters. The mixolimnion stratified normally. Lake Lenore has a maximum length of 9.2 km., an area of 556 ha., a maximum depth of 11 m. and a salinity of 14 gm. per liter of total dissolved salts. The lake showed a slight vertical temperature gradient during the spring but for the most part was homothermal throughout the year. The pH of both lakes was near 10 and the dominant ions were sodium, carbonate, sulfate and chloride. The zooplankton consisted of *Moina hutchinsoni* Brehm, *Pedalia fennica* (Levander) and *Brachionus plicatilis* Müller in Soap Lake, and *Moina hutchinsoni* Brehm, *Pedalia fennica* (Levander), *Diaptomus sicilis* Forbes and small numbers of *Diaptomus nevadensis* Light in Lake Lenore. The phytoplankton population of Lake Lenore consisted chiefly of *Amphora* sp. and *Chaetoceros elmorei* Boyer whereas the qualitative makeup of the Soap Lake phytoplankton population is unknown due to difficulties encountered in preservation described below.

The zooplankton population was sampled with a Clarke-Bumpus sampler and the phytoplankton was separated from Kemmerer water samples by centrifuging. Chlorophyll was determined on acetone extracts of filtered plankton. The zooplankton samples were preserved in the usual way by the addition of formalin to make a concentration of approximately 4 percent. Apparently the high alkalinity of the water prevented preservation either by destroying the formalin or by dissolving the soft parts of the animals despite the presence of formalin. By the time the entire series of samples had been accumulated and time was available for making counts, considerable deterioration had taken place. The phytoplankton samples, preserved in Transeau's solution, remained in satisfactory condition in the Lake Lenore series but were in such a state of deterioration in the Soap Lake samples that cell counts could not be made. Therefore, estimates of the phytoplankton population for Soap Lake were based solely on the chlorophyll measurements. Details of the technique and results are given in the works cited in the bibliography (Comita 1953; Anderson 1954; Engstrom-Heg MS.).

In Soap Lake the phytoplankton population, as estimated from the chlorophyll extracts, was high during the fall, winter, and early spring but was low at other times

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[1] The authors are grateful to Dr. W. T. Edmondson for much suggestion and comment and to the Department of Zoology of the University of Washington for facilities used in the investigation. Financial support was received from the State of Washington Research Fund in Biology and Medicine. Assistance with the identification of diatoms was kindly provided by Dr. R. Patrick and Mr. H. E. Sovereign.

FIG. 3. Distribution of roots of tall wheatgrass, and of alkalinity, salinity and sodium at various levels in 2 trenches. The first profile, left, contained roots of a few suppressed plants of saltgrass which were not distinguishable from the wheatgrass roots. Rhizomes of saltgrass were as deep as 27 inches.

Root ends of 3 orders were recognized in charting. Unbranched rootlets are shown as a dot (.), once branched as a circle (O), and those with branched branches thus (O—).

The underlining of figures in the "% salt" column indicates total salt concentration at or above the theoretical tolerance of plants.

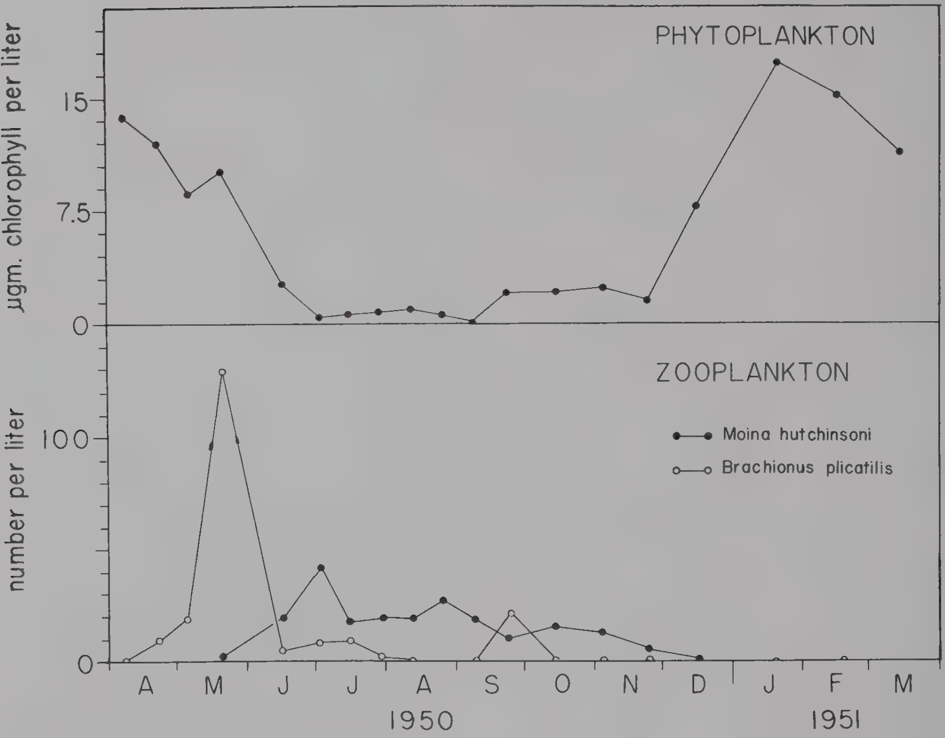

FIG. 1. Seasonal variations of the phytoplankton and zooplankton populations in the mixolimnion of Soap Lake, April 1950 to March 1951.

(Fig. 1). During May, 1950, the phytoplankton population decreased rapidly and at the same time the population of *Moina* began to increase. By the time the *Moina* population had reached its yearly maximum early in July the chlorophyll concentration had been reduced to a summer minimum. Sexual reproduction then set in and the population of Cladocera declined, reaching its yearly minimum in January, 1951. During this period there were two sharp increases but the general trend was that of decrease. The rotifier population was high just before and during much of the period of *Moina* abundance. Early in December when the *Moina* population had reached a low level there was a resurgence of the phytoplankton population which grew rapidly to a maximum in January. Thus there was a clear reciprocal relationship between the population densities of Cladocera and phytoplankton.

The situation in Lake Lenore was more complicated in that there were two maxima in the phytoplankton population, one in April, dominated by *Amphora,* and one in September, dominated by *Chaetoceros* (Fig. 2). The maximum population in April rapidly declined to the yearly minimum in June, during which period there was a large increase in the copepod population, especially *Diaptomus sicilis*. At the time of maximum copepod abundance, there was also a dense population of *Moina.* Both zooplankton populations declined rapidly during July and early August, reaching a minimum in the middle and latter part of August. During this period of decline the phytoplankton grew rapidly, achieving its second peak of population abundance early in September. Shortly after this, a rapid decline in the phytoplankton population was accompanied by a resurgence of rotifers and of Cladocera which was followed by another small resurgence of copepods in October. By the middle of December all zooplankters were at a low concentration and the phytoplankton was again increasing.

The most probable interpretation of these results involves a control of population size of the phytoplankton by the grazing activity of the zooplankton. Unfortunately, data are not available on the rate of photosynthesis of the phytoplankton populations, but in view of the fact that both lakes have a large supply of nutrients at most times, it is very unlikely that the decline in phytoplankton population can be attributed wholely to lack of nutrients. Moreover, it is doubtful that the large population of animals could have been maintained in an active state of growth during the entire summer if the phytoplankton population had not been reproducing. The animals were well fed, judging by their appearance. The recent work of Ryther (1954) has shown that reproduction and growth in *Daphnia* can be inhibited by a senescent *Chlorella* population. In Lake Lenore the existence of a large population of copepod nauplii which were metamorphosing rapidly by the time the diatom maximum occurred in April suggests that this effect was not operating significantly. Whether the changes described here can be attributed to auto-inhibitory effects cannot be decided from our data;

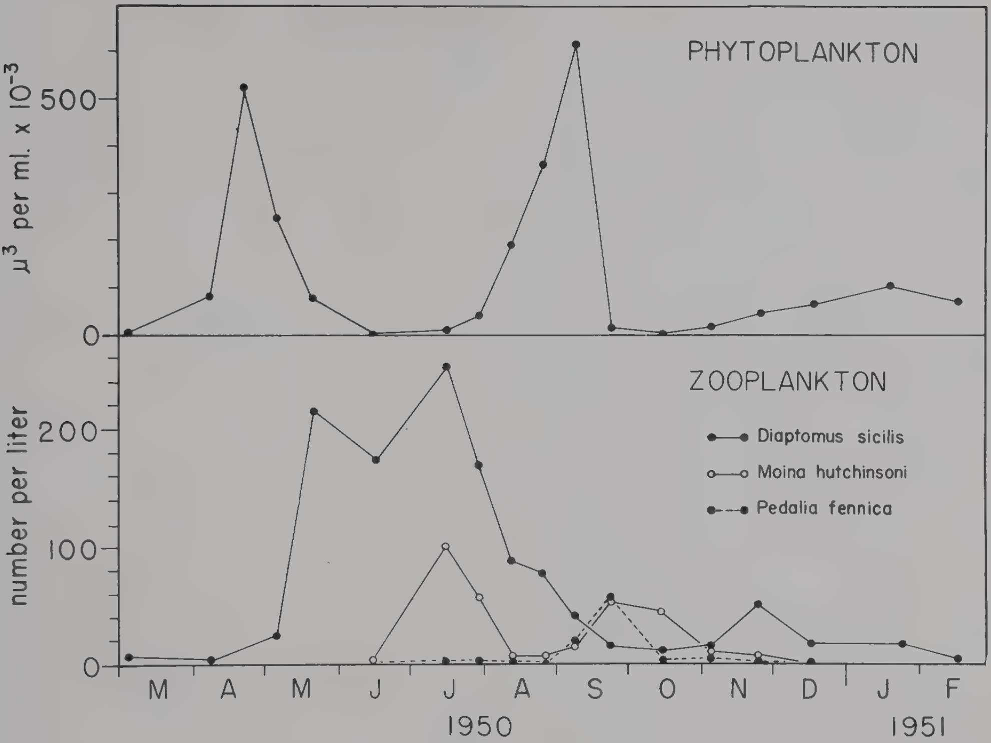

FIG. 2. Seasonal variations of the phytoplankton and zooplankton populations in Lake Lenore, March 1950 to February 1951. Copepod nauplii not included.

nevertheless, it would seem likely that if auto-inhibition was the primary cause of the changes, the lakes would not have been devoid of other species for such long periods during the summer. In any case, the data are consistent with the concept of control by grazing.

SUMMARY

1. The seasonal changes in the phytoplankton and zooplankton populations were studied in Soap Lake and Lake Lenore, two highly saline lakes in central Washington, during the period March 1950 to March 1951.

2. In Soap Lake, the phytoplankton population was large during the fall, winter, and early spring but was small at other times. The zooplankton, which consisted of *Moina, Pedalia* and *Brachionus,* were in abundance during the summer period of phytoplankton minimum and a clear reciprocal relationship was observed between population densities of Cladocera and phytoplankton.

3. In Lake Lenore, there were two maxima in the phytoplankton population, one in April, dominated by *Amphora,* and one in September, dominated by *Chaetoceros.* A large population of *Diaptomus* and *Moina* was maintained during the midsummer phytoplankton minimum. The decline of the summer zooplankton was followed by the second phytoplankton maximum which was in turn followed by a resurgence of *Pedalia* and *Moina* and a further small pulse of *Diaptomus.*

4. A control of phytoplankton population size by the grazing activity of the zooplankton is given as the most probable interpretation of the seasonal changes observed.

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DETERMINATION OF THE NUMBERS OF SOIL MICROORGANISMS BY THE USE OF MOLECULAR MEMBRANE FILTERS[1, 2]

The use of membrane filters for the removal of microorganisms from liquids was introduced by Fick exactly 100 years ago (Ferry 1936). Numerous improvements suggested by different investigators recently culminated in the development of special nitrocellulose molecular filters which preclude lateral diffusion of colonies and are adapted for large scale production (Zsigmondy and Bachman 1918, Zsigmondy 1922, Goetz 1947). The technique developed by Goetz (1951) was used in a series of controlled experiments by Clark and his associates (Clark, *et al.* 1951) and was found to possess definite advantages in bacteriological analyses of polluted waters. In the opinion of these investigators, the filtration method promises reduction in time and labor, as well as a greater precision than is achieved by methods now in use.

A few trials conducted by the writers have indicated that the method employing membrane filters may be applied in soil analyses performed at present by means of agar plate counts. The latter technique leaves much to be desired in regard to the convenience of recording the colonies and the variation betwen duplicate tests. In order to evaluate the relative merits of the two methods, samples of biologically active soil layers were subjected to simultaneous analyses using different dilutions and as many as 10 duplicate determinations.

The analyzed soil materials included the surface horizon of a prairie silt loam of the Carrington series, a humus-enriched layer of a hardwood silt loam of the Miami series, and partly decomposed hardwood-hemlock duff (F-layer) of a morainic podzol of the Kennan series.

The samples were passed through a 20-mesh sieve, and 50 cc portions were incubated in petri dishes for 48 hours at field capacity and 23° C. One cc of the incubated material was taken by a calibrated scoop and dispersed in 199 ml of sterile distilled water in a Waring blender for 30 seconds. The suspension was diluted with sterile distilled water in proportions 1:5,000, 1:50,000, and 1:500,000. Determination of colonies by the plate count method was made on an agar medium following standard procedure (Fred and Waksman 1928). Double strength Albimi M peptone with 0.5 per cent lactose, according to Clark, *et al.*, was used as the nutrient solution; the plates were incubated at 30° C for 6 days. For the determination of colonies by the membrane method, a filter was placed in a sterilized stainless steel funnel (Figure 1), and a 100 ml aliquot of the suspension was drawn through with the help of an electric vacuum pump.[3] The filter was immediately transferred to a sterile petri dish containing an absorbent pad saturated with Albimi M peptone nutrient solution. Petri dishes were incubated at 30° C for 48 hours and colonies recorded by means of a microbiological counter.

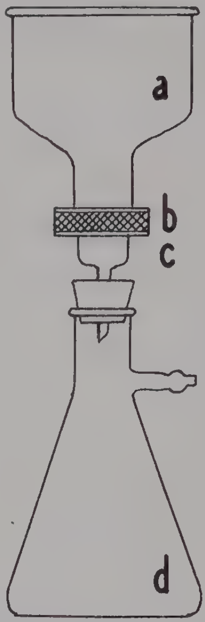

FIG. 1. Filter apparatus for the determination of aerobic and anaerobic microorganisms; a. stainless steel funnel accommodating suspension of organisms; b. connecting lock-nut; c. support for the molecular filter membrane; d. suction flask attached to an aspirator.

The results obtained with 1:5,000 dilution are reported in Table I. The values for standard deviation and coefficient of variability for each set of data indicate that the filter membrane method is reproducible within much narrower limits than the agar plate method.

As might be expected, increasing the dilution to 1:50,000 amplified the differences between the duplicate determinations. At this rate of dilution, the value of the coefficient of variability for agar plate determinations ranged from 27.9 per cent to 64.9 per cent; similar values for the filter membrane determinations ranged from 14.7 per cent to 18.6 per cent. The number of colonies obtained with 1:500,000 dilution was too small to yield suitable data.

Soil analyses by the filtration method are somewhat slower than those by agar plate counts. The comparatively high cost of molecular filters is another disadvantage of the membrane method; this, however, is of minor importance in analyses which aim at more accurate determination of certain groups of organisms. The filter membrane technique is primarily adapted to the determination of aerobic and anaerobic bacteria; its merits in the determination of fungi without suitable modifications are questionable.

The study of specific groups of soil microorganisms can be conducted with the aid of many selective media as well as antibiotics. Until now the authors used largely

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[1] Contribution from the Soils Department, Wisconsin Agricultural Experiment Station in cooperation with the Wisconsin Conservation Department. Publication approved by the Director of the Wisconsin Agricultural Experiment Station.

[2] The writers are indebted to Dr. Harold F. Clark, Bacteriologist of the U. S. Public Health Service, Cincinnati, Ohio, for his instruction in the use of the membrane filters technique.

[3] The equipment as well as the filters may be procured from the AG Chemical Co., Pasadena, California.

TABLE I. *Number of thousands of cells of aerobic bacteria per cc of soil material determined by means of the agar plate count and molecular filter membrane methods using doube strength Albimi M peptone medium plus 0.5 per cent lactose at 1:5,000 dilution*

Test number	Prairie soil		Forest soil		Hardwood-hemlock duff	
	Plate count	Filter count	Plate count	Filter count	Plate count	Filter count
1	380	765	765	1970	410	900
2	305	665	485	2060	210	1020
3	200	705	415	1755	240	1260
4	590	835	*	2165	130	1170
5	*	770	*	2050	85	1065
6	115	715	460	2065	505	1040
7	300	775	450	2305	475	735
8	170	845	915	2000	440	825
9	*	580	*	2185	410	735
10	*	815	*	2265	470	785
Mean	294.3	747.0	581.7	2082	337.5	953.5
St. dev.	± 158.8	± 82.2	± 207.3	± 158.8	± 158.2	± 185
Coef. var.	54.1%	11.0%	35.5%	7.6%	46.9%	19.4%

*Impossible to count because of the indistinct outline of bacterial colonies or the spread of fungal mycelia.

two media: (1) sterilized extract of a fine textured hardwood soil, A_1 horizon, 1 volume of soil to 9 volumes of distilled water, with 0.5 g K_2HPO_4 and 1 g. of glucose per liter; (2) Albimi peptone solution including 40 g peptone, 6 g yeast autolysate, 3 g K_2HPO_4, and 5 g NaCl per liter of distilled water. The first solution favors the growth of fungi and the second the growth of bacteria. For the survey of humus populations, a sterilized weak extract of hardwood-hemlock arthropod ectohumus reinforced by dextrose was found to be a suitable medium. For the determination of anaerobic bacteria the filters must be incubated for 7 days in a sealed jar with germinating oats.

The outlined technique was used for the evaluation of microbiological properties of ectorganic and endorganic layers of several well established types of forest humus (Mader 1943, Wilde 1954). This study was supplemented by the determination of fungi by the plate method with Rose bengal agar, a medium which suppresses the development of bacteria and the spread of fungal colonies. The results, summarized in Table II, reflect conspicuously the mode of humus layers' development and the ecology of the habitats from which the humus samples were obtained.

TABLE II. *Population density of microorganisms in different types of forest humus as determined by the use of molecular membrane filters and by agar plate counts on several nutrient media*

Humus type	Molecular membrane filter				Plate count Rose bengal agar
	Soil extract		Albimi peptone		
	aerobic	an-aerobic	aerobic	an-aerobic	
	cells x 10^6/cc				
Scrub oak rhizogenous sand mull (Boscobel, Wisconsin)	0.16	0.01	2.09	0.95	0.006
Maple-basswood Lumbricus crumb mull (Marshfield, Wisconsin)	0.45	0.33	0.20	1.24	0.280
Black ash saprogenous fen mull (Gagen Experimental Forest, Wisconsin)	0.54	0.23	2.56	0.91	0 012
White-black spruce arthropod fine mull (Hearst, Ontario)	0.30	0.01	1.20	1.70	0.007
Maple-basswood ectendorganic duff-mull (Menominee Indiand Reservation, Wisconsin)	0.12	0.20	35.80	0.00	0.112
Hemlock-yellow birch arthropod bran-mor (Clear Lake, Wisconsin)	0.43	0.01	21.40	0.06	0.310
Hemlock partly lignified mycelial mor (Filibert Roth, Michigan)	0.32	0.09	0.40	0.38	0.220
Balsam fir-white spruce saprogenous mor (Iron Mountain, Michigan)	0.16	0.06	8.10	7.80	0.290
Black spruce Sphagnum moss mor (Franquelin, Quebec)	0.17	0.02	1.76	0.51	0.090
Jack pine-Cladonia crust mor (Dorro Couche Dune Station, Wisconsin)	0.38	0.00	5.50	0.02	0.670

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A TIME REVISION OF THE PLEISTOCENE POLLEN CHRONOLOGY OF SOUTHEASTERN NORTH CAROLINA[1]

On the basis of the radiocarbon data then available the author (Frey 1953) published a chronology for the stratigraphy of the Carolina bays in southeastern North Carolina, in which the uppermost organic layer (the one still accumulating in present time) with a radiocarbon age of approximately 10,000 years near its lower boundary (sample C-474, in Libby 1951) and a pollen spectrum indicating a marked amelioration of climate from the preceding pine-spruce phase, was assigned to post-Mankato time. The two lower organic horizons, each with a C^{14}-age greater than 20,000 years (samples C-475 and C-476, in Libby 1951), were tentatively assigned to the Tazewell-Cary and Peorian intervals, respectively. Except for the uppermost organic stratum the entire column was believed at that time to date from the Wisconsin Glacial, because of the continuous occurrence of spruce pollen, and because the sedimentary record appeared to be essentially continuous. In the two succeeding years additional studies and data have required a revision of this chronology, resulting in the several lower horizons being much older than previously believed.

The radiocarbon age of the middle organic layer at Singletary Lake is now known to be greater than 38,000 years (sample W-197, in Rubin and Suess 1955, = C-475, in Libby 1951). The sample concerned was collected on 18 March 1950 with an ordinary Davis peat sampler from the 4-inch stratum between 16 ft. 10 in. and 17 ft. 2 in. The sample as analyzed was composited from 45 separate "shots" with the sampler. In spite of this heterogeneity, which Deevey and Potzer (1951) deplore in pollen studies, in spite of the increased opportunity for contamination with younger carbon from nearer the surface, and in spite of the rather considerable time the sample had been stored in a dry state before analysis, during which time it could possibly be carrying on some carbon exchange with the atmosphere, the C^{14}-age is still near or beyond the limit of sensitivity of the acetylene method recently developed by Suess (1954a). The apparent radiocarbon age of such a sample could be increased only by dilution with older organic matter through secondary deposition. Although it is now known that secondary deposition is currently going on in the bay lakes and probably has gone on in the past, this source of contamination is not believed to have been sufficient to materially increase the radiocarbon age of the sample being considered, and hence to affect the conclusions of this paper.

At a location such as this far beyond the maximum advance of the glaciers there obviously are no layers of till or drift to help infer the age of a particular organic stratum. Perhaps the clay-silt horizons in the bays consistently represent glacial stages, but conclusions on this matter are still premature. The chief basis for inferring the age of these several strata is the climatic changes indicated by major fluctuations in the pollen spectra of the strata, the supposition being that major changes in climate will modify the vegetation of a region and that this will be reflected in a change in the pollen spectra. During the Pleistocene such major climatic changes are certainly correlated with the successive advances and retreats of the glaciers.

Recently the author (Frey 1954) and Wells and Boyce (1953) independently arrived at the same conclusion that the bay lakes in North Carolina are currently expanding their surface areas through peripheral erosion of their organic margins. The implication of this, as apparently demonstrated particularly well by the pollen diagram from Little Singletary Lake (Frey 1953), is that an unknown quantity of secondary pollen and other microfossils is currently being sedimented on the bottom along with the primary pollen of present origin. Depending on the extent to which this is going on now and has gone on in the past, the pollen diagrams are composite in origin, and cognizance must be taken of this factor in interpreting the diagrams. Nevertheless, the general similarities between the diagrams from eight neighboring localities, as described in the previous paper (Frey 1953) are close enough and specific enough, including the mass occurrence of particular pollens and spores at particular levels without appreciable percentages above and below, that they validate the regional pollen succession as real and not merely the result of the successive coincident reworking of the sediments during various periods of erosion. The author believes that the quantity of secondary pollen derived from the reworking of sediments has not been sufficient to obscure the gross, and even some of the more subtle, real changes in the pollen succession that have occurred.

In all three organic horizons the pollen diagrams demonstrate an amelioration of climate, which is believed associated with a phase of glacier retreat or even with an interglacial age. Whereas two years ago it seemed reasonable that the several advances and retreats of the Wisconsin ice sheet (as commonly understood) were correlated positively with changes in the climate and forest composition in North Carolina, it is now quite certain that they were not, either because the climatic ameliorations associated with these retreats were not great enough or not of sufficient duration.

Flint and Rubin (1955) have carefully considered the pre-Mankato radiocarbon dates published by Suess (1954b) and Rubin and Suess (1955) and have concluded that there were possibly two major phases of glaciation in Wisconsin time. The more recent glaciation began with the deposition of the Farmdale loess some time prior to 25,000 years ago. The Tazewell and Cary represent substages within this major advance. Since the middle organic stratum of Singletary Lake has a radiocarbon age beyond the limits of this glacial interval, and since there are no marked changes in the pollen diagrams from any of these localities within the clay-silt stratum between the middle and upper organic horizons, it appears that any broad periglacial changes in climate associated with the advances and retreats of the glacier within Wisconsin time (*sens. str.*) either were not great enough or not of long enough duration to materally affect the forest vegetation in coastal North Carolina.

Evidence for an earlier major glacial advance in pre-Farmdale and post-Sangamon time is based largely on a single sample from Ohio. The till concerned is leached to a depth of 48 in., suggesting a period of weathering of roughly 16,000 years. On the basis of the post-Mankato vegetational changes that have occurred in North Carolina, such a period of time, if accompanied by a comparable amelioraion of climate, should have witnessed a marked change in the vegetation of the Southeast. Rubin and Suess (1955), referring briefly to the paleo-temperatures in the Caribbean determined by Emiliani from O^{16}/O^{18} ratios, noted that the temperature of the surface water in the Caribbean began to increase suddenly about 12,000 years ago, after having been about 5° C. colder than present temperatures for a long period of time (duration not stated). If this period of time included the pre-Farmdale interval, as conceived by Flint and Rubin, then the North Carolina vegetation may have continued essentially unaltered through the interval.

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[1] Contribution No. 593, Department of Zoology, Indiana University.

The major point of this note is that the two lower organic layers in Singletary Lake (and the other Carolina bays as well) antedate the Wisconsin Glacial, as commonly conceived. If the middle horizon is contemporaneous with the post-Sangamon: pre-Farmdale interval, then the lowest organic horizon may well date from Sangamon time. Whereas, if the middle layer dates from the Sangamon, then the lowest layer might logically be associated with the Yarmouth. The latter relations, if true, would necessitate a revision of our thinking regarding the age of the various Coastal Plain "terraces." Singletary Lake, at an elevation of 63 ft., occurs just about at the location of the Surry scarp, as mapped by Flint (1940). The scarp is commonly considered Sangamon in age, which would make the lowermost sediments in Singletary Lake supposedly older than the sea covering them. No marine influence has yet been detected in the sedimentary record.

A disturbing feature is the small length of the sedimentary column for such a long interval of time and the fact that spruce is present in small percentages throughout the two lower organic horizons. It would appear that there undoubtedly are discontinuities in the record that have been obscured by secondary deposition, resulting among other things in the small representation of spruce, since it is unlikely that spruce persisted in the Southeastern Coastal Plain during an interval as long and as mild as the Sangamon is believed to have been. The quantity of spruce pollen in the middle and lower organic strata may furnish an index to the extent of secondary deposition. In a previous paper (Frey 1953) the ratio of intact to fragmented pine grains was suggested as being suitable for the same purpose. The low pine ratios in the middle organic layer were suggested as having resulted from increased activity of the benthos during a more eutrophic phase of the lake, but conceivably they could also have been affected by secondary deposition.

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PRELIMINARY NOTES ON THE CORRELATION BETWEEN AKALINITY AND THE DISTRIBUTION OF SOME FREE-FLOATING AND SUBMERGED AQUATIC PLANTS

An attempt is made, in the present paper, to correlate total alkalinity with submerged and free floating aquatic plants in four habitat types in southeastern Louisiana. Collections were made over a period of 4 months (February, 1949, to May, 1949) throughout the New Orleans area.

The literature available on such work as this for inland waters (lakes and ponds) is very meager. Pearsall (1921) in England did a similar study in which he divided lake waters into two types, calcareous and alkali. The calcareous type water had a low $K + Na/Ca + Mg$ ratio due to large quantities of calcium salts and was rich in nitrates, carbonates, silica, etc. The alkali water was usually associated with a scarcity of dissolved mineral substances and poor in nitrates and silica. The higher, floating plants (such as *Lemna, Stratiotes*) were confined to the former type water in England.

Alkalinity tests were made according to the methods outlined by American Public Health Association (1946), and Welch (1935). In this test, one titration served to indicate the amount of hydroxide, carbonate and bicarbonate present, expressed as parts per million of calcium carbonate.

Plant identification essentially follows that of Fassett (1940) although there is an occasional deviation to that of Muenscher (1944).

The four habitat types represented are: 1. temporary pine land ponds; 2. flood plain bayous in the process of drying up; 3. flood plain lagoons; 4. abandoned bottom and drainage projects.

Type 1 habitat (temporary pine land ponds)—This is an area of longleaf pine flats east of Lake Pontchartrain (Slidell) in the Prairie Terrace of the Pleistocene deposits. The soil is sandy with high clay content near the surface which makes for a poorly drained area. The vegetation is chiefly one of loblolly (*Pinus taeda* L.) and longleaf (*Pinus australis* Michx.) pine with several scrub oaks.

All collections came from roadside ditches except one from a marsh which was subject to salt water influences.

Table I. *Plants collected in various habitat types in the New Orleans area*

Plants	Habitat types			
	1 Pine land ponds	2 Flood plain bayous	3 Flood plain lagoons	4 Bottom land drainage
Anacharis densa (Planchon) Victorin	..	..	x	..
Azolla caroliniana Willd.	..	x	x	..
Cabomba caroliniana Gray	..	..	x	..
Ceratophyllum demersum L.	..	..	x	..
Lemna spp.	..	x	x	..
Lemna minima Philippi	..	..	x	x
Lemna minor L.	..	..	..	x
Lemna valdiviana Phillippi	..	..	..	x
Myriophyllum spp.	x	..	..	..
Myriophyllum brasiliense Cambess.	x	.	..	.
Myriophyllum humile (Raf) Marong.	x	..	..	
Najas guadalupensis (Spveng) Marong.	x	..	x	
Pistia stratiotes L.	..	..	x	..
Potamogeton crispus L.	..	..	x	..
Potamogeton pusillus var. *typicus* Fernald.	..	..	x	x
Proserpinaca pectinata Lam.	x	..	..	..
Ricciocarpus natans (L.) Corda	..	x	..	..
Riccia fluitans L.	..	x	..	..
Utricutaria spp.	..	..	..	x
Utricularia gibba L.	..	..	x	..
Wolfiella floridana (Smith) Thompson	..	x	..	..

Water depth at collecting points ranged from 6 inches to 1 foot.

Type 2 habitat (flood plain bayous in the process of drying)—These drying bayous are in the Mississippi Alluvial Plain which is one of fine textured alluvial deposits. The areas are entirely dry through the summer months and are progressively becoming drier due to filling in. Collections were made in the city limits of New Orleans. Depth of water at collecting points ranged from 2 inches to 1 foot.

Type 3 habitat (flood plain lagoons)—These lagoons are in New Orleans and are subjected to a great deal of disturbances due to fact that they are in the public parks. The soil type is the same as in Habitat type 2. Depth of water at collecting points ranged from 6 inches to 2 feet.

Type 4 habitat— This is an abandoned drainage project on the west bank of the Mississippi (Waggaman Pond) previously a cypress-tupelo gum swamp. It was drained and under cultivation for about 10 years before being abandoned in 1919. The soil type is the same as Habitat type 2. Depth of water at collecting points ranged from 1 inch to 3 feet. *Utricularia* spp. was taken on a mat of *Eichornia crassipes* (Mart) Solms and *Alternanthera philoxeroides* (Mart) Standley.

Discussion

Habitat type 1 may be characterized as one of low bicarbonate (Table II) content with no hydroxides or carbonates present. The most striking aspect of this water type is the presence of plants of the genus *Myriophyllum* and *Proserpinaca* which occurred in great numbers.

Table II. *Alkalinity expressed as ppm. of calcium carbonate*

Habitat type	Where sample taken	Hydroxide	Carbonate	Bicarbonate
1	1 mile west Slidell	0	0	31
	Slidell	0	0	34
2	Near City Dump (Sauvage)	0	0	112
	Old Gentilly Highway	0	0	237
3	Audubon Park	0	10	63
	City Park	0	24	37
4	Waggaman Pond	0	6	82

Habitat type 2 may be characterized as one of high bicarbonate content with no hydroxides or carbonates present. The most striking aspect of this type was the occurrence of Bryophytes such as *Riccia* and *Ricciocarpus*.

Habitat type 3 may be characterized as having a medium bicarbonate content, a low carbonate content and no hydroxides present. This type supports the most varied range of aquatics and appears to be in the range of tolerance of the greatest number of plants.

Habitat type 4 may be characterized as being similar to type 3 but representing a greater diversity in carbonate, and bicarbonate ranges, that is, the carbonates were lower than in type 3 and the bicarbonates higher than in type 3. The vegetation supported here does not represent as great a diversity as found in type 3.

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ON THE METHODS USED BY THE STARFISH *PISASTER OCHRACEUS* IN OPENING THREE TYPES OF BIVALVE MOLLUSCS

The method by which starfish feed on healthy bivalve molluscs has been widely discussed, but it is still poorly understood. It has been suggested that: the starfish might pull the shells of a bivalve apart (Schiemenz 1895-97), the sea star might take the bivalve by surprise and catch it before it is able to close (Schiemenz 1895-97), a poison might be secreted by the starfish which would relax, weaken, or kill the mollusc (Aldrich 1954; Sawano and Mitsugi 1932; Van Der Heyde 1922), a boring mechanism might be used to make an opening in the shell for the insertion of the stomach (Forbes 1841), and the starfish might cover the siphonal region of the bivalve and kill the animal by suffocation (Reese 1942). Recent work on the common Pacific Coast starfish, *Pisaster ochraceus,* has brought to light some new evidence concerning this old question.

Early in the study an important question was raised: does *Pisaster* really have to pull open a bivalve mollusc in order to feed on it? An examination of mussels, *Mytilus californianus,* being fed upon in the field has indicated that the larger mussels frequently remain closed during a great part of the feeding process and that they often do not gape until considerable digestion has taken place. In fact, a number of mussels have been observed with their valves closed even though a starfish had digested practically all of the soft parts except the posterior adductor muscle. In these cases the starfish were feeding with their oral regions pressed tightly against the ventral valve edges of the mussel. A close inspection of this region reveals an important point. The shells are not perfectly sealed here but instead have a permanent opening where the byssus threads protrude between the two valves. This slit may measure as little as 0.5 mm in width in the smaller mussels and as much as 3.2 mm in the larger animals. The Pismo clam, *Tivela stultorum,* is considered to be a tightly sealed bivalve mollusc, and yet it also has an opening between the valves both anteriorly and posteriorly, measuring between 0.1 mm and 0.6 mm. Fourteen additional species of Pacific coast clams have been examined, and it has been found that they all have an opening in the shell posteriorly that is large enough for the insertion of a *Pisaster* stomach. Although these openings in both the mussel and the Pismo clam are partially blocked by the pliable periostracum, it has been found that the starfish can readily peel this back in the feeding process. No opening of this nature has been found in the oyster, *Crassostrea gigas,* but an examination of freshly cleaned shells has indicated that the valves are not perfectly sealed.

Since it was impossible to be certain that the mussels in the field, noted above, were closed throughout the entire feeding, experiments were devised to ascertain if *P. ochraceus* could actually take advantage of the opening in the byssus region if the shells had remained closed. Mussels were tightly bound with stainless steel wire and placed in a tank with some starfish. The sea stars readily accepted these bound animals and fed on them by inserting their stomachs through openings as narrow as 0.5 mm, sometimes extending their stomachs as much as 7.0 cm within the mussel shells. In a number of cases all of the soft parts were completely digested by *Pisaster* even though the molluscs were closed maximally throughout the entire feeding. Similar experiments were also tried with the Pismo clam, and the starfish inserted its stomach through openings as narrow as 0.4 mm in order to digest the mollusc. Recently two wire-bound oysters were fed upon by *P. ochraceus.* The stomach was inserted between the two valves even though the slit penetrated was less than 0.2 mm wide, and the shell margin in the area entered was unbroken. In each case the sea star digested over one half of the oyster soft parts, and a large mass of stomach was found within the valves.

Pisaster ochraceus does not have to assume the characteristic humped-up pose, said to be essential to the feeding process (Flattely and Walton 1922; Ricketts and Calvin 1939; Schiemenz 1895-97; Yonge 1949) when it is feeding on a clam, mussel, or an oyster. It has been demonstrated 34 times that experimentally prepared one-, two-, and three-armed starfish are able to feed on mussels and oysters even though they generally are unable to orient their arms in a pulling position. In most of these cases the starfish attached themselves along the valve edges with their stomachs inserted through the opening at the byssus region of the mussels or at any region of the oysters. In addition, large starfish very often have been observed feeding on mussels, clams, or oysters even though they were not in a position suitable for an effective pull. For example, occasionally a starfish has been found feeding on one member of a clump of oysters, and the sea star was attached on the surface of the oyster group in such a way that it could not exert a pull on the valves of the particular oyster on which it was feeding. Its stomach was inserted between the shells of the single individual.

All of these points have made it clear that *P. ochraceus* does not need to pull open a bivalve mollusc in order to feed on it. Individual starfish are capable of inserting their stomachs through crevices less than 0.2 mm in width and can completely digest all of the soft parts within the closed shells. However, mussel and oyster valves often do gape shortly after the sea stars have begun to feed, and this must be explained if a complete picture of the starfish feeding process is to be obtained. There are a number of possible explanations for this as suggested at the beginning of this paper. Since pull has been cited in most textbooks as the means by which starfish are enabled to eat bivalves, we will consider this possibility first. Occasionally a large mussel, with its valves gaping, has been found with its siphonal region tucked into the starfish oral area. Also, it has been noticed that mussels 2-4 cm in length often gape within 15-20 minutes after they have been drawn into the feeding position by the starfish. When, in both of these situations, the tube feet of the starfish were cut early in the feeding process, the shells usually closed. However, the valves of small mussels in the size range noted above had very often been opened so widely by the starfish that the adductor muscles were actually torn. Thus, it is clear that *P. ochraceus* can pull open small mussels readily, and possibly they also can open the larger ones or at least hold the shells open by means of pull.

In order to determine experimentally the magnitude of pull exerted by *P. ochraceus,* a series of mussels had their adductor muscles cut. They were bound tightly with rubber bands and placed in a tank with starfish. When a mussel was found gaping, while being fed upon by a starfish, the amount of the gape was measured with a vernier caliper and the number of grams of force needed to duplicate this opening was determined. By using this technique it was found that starfish, of approximately 30 cm in diameter, could generally exert a pull of 1200 to 2600 grams. Two cases were recorded in which forces of 3400 and 4000 grams respectively were exerted. Schiemenz (1895-97), using a very different technique of measurement, found that *Asterias glacialis* could exert a force of at least 1350 grams.

A force of 4000 grams exerted at the ventral byssus region, where a good many feeding starfish attach, can generally open mussels up to 10.0 cm in length, but several hours of pull may be needed to cause the valves to gape in those of the 9.0 to 10.0 cm range. However, small mussels require much less pull than this, and those up to 4.0 cm in length can be opened with as little as 600 grams pull in a few seconds. Experimental evidence to date has indicated that if the force is exerted at the posterior region, directly over the posterior adductor muscle, a large mussel can be opened more effectively with any given weight. In this respect, it is of interest to recall that in all cases of *P. ochraceus* having apparently pulled open large mussels, the starfish was attached at the posterior region.

It has been shown that *P. ochraceus* can exert a pull of considerable magnitude and that it can use this force in the feeding process. However, all cases of early shell gaping cannot be explained in terms of pull; voluntary opening of the valves also appears to be an important factor. From a functional point of view it is essential for a bivalve to keep its shells open at least part of the time when it is submerged; consequently, it was interesting to discover that mussels, oysters, and Pismo clams commonly open their shells while the starfish stomach is within their valves digesting the soft parts, and yet these same specimens close their shells readily and completely following the light touch of a probe on the mantle. In addition, it has been noted that mussels or clams will close their shells slightly or not at all when being touched or moved by a *Pisaster*. Also large mussels often open their shells while they are being subjected to a pull of as much as 4000 grams, yet they will readily close when touched, even under this tension. This latter tendency was also noticed by Reese (1942) in his experiments on the clam *Venus* and the oyster. He found that, "In some cases the valves opened for a millimeter or two within a few minutes (after a mechanical pull was exerted), but when the valves were tapped with a pencil they snapped together instantly. In general this more-or-less sudden closure of the valves when tapped occurred even after several hours or even days." Since the stimulus of a starfish as well as strong mechanical pull does not appear to overcome the natural tendency of the bivalves studied to gape, it appears that voluntary opening on the part of these molluscs must play an important role in the feeding process of the starfish. Certainly we do not have the factor of surprise acting here, rather we have an apparent lack of sensitivity of the bivalve to contact with and slow movement of the starfish.

The possibility of *P. ochraceus* utilizing a toxic substance in its feeding mechanism cannot be overlooked. A toxin has been demonstrated in stomach extracts of *Asterias amurensis* by Sawano and Mitsugi (1932). Aldrich (1954) has clearly been able to produce relaxation of the adductor muscles of *Mytilus edulis, Modiolus demissus plicata,* and oysters using water extracts of the pyloric diverticula of *Asterias forbesi* in concentrations as low as 1%. However, tests made with extracts and portions of the stomach and pyloric diverticula of *P. ochraceus* have shown no significant poisonous or narcotic effects on a mussel or a Pismo clam. Mussels so treated showed normal behavior, and they responded readily to light mechanical stimuli. A slight increase in frequency and a decrease in amplitude of heartbeat was noted in the Pismo clam following the administration of stomach extracts from a recently feeding starfish. *Pisaster ochraceus* can digest the soft parts of a bivalve mollusc without apparently disturbing its activities to any great extent. As noted earlier, partially digested mussels, Pismo clams, and oysters in the process of being consumed, frequently respond readily to a touch on the mantle by closing. In one case, a mussel 18.0 cm long was fed upon intermittently, but frequently, for 25 days by three small starfish about 5.5 cm in diameter. During this period the mussel was observed opening and closing its valves in a relatively normal fashion, yet an examination of the mussel at the end of this time showed that about one third of the soft parts had been digested. Thus, although a process of narcotization is possible as indicated by the non-sensitivity of the bilvalve to starfish contact, the important point is that a poison affecting the general response mechanisms and general activities of the mollusc is apparently not being formed.

Concerning the possibility of a boring mechanism, mentioned previously, it has been known for many years that the small round holes in bivalve shells are caused by the action of carnivorous snails and not starfish. In regard to the theory cited in Reese, (1942) that "A starfish fastens its suckers on any oyster, and then the stomach covers the edge of the oyster's shell with the result that the currents of water are stopped and the animal within the shell is killed by suffocation," I have been able to demonstrate that medium-sized mussels can be kept forcibly closed without ill effects for 24 to 120 hours. Oysters have been maintained in an aquarium for two days with their valves bound tightly with wire, and yet they recovered when the wire was removed. This far exceeds the short space of time required by *Pisaster* to open the shells or initiate digestion. Thus, suffocation can be ruled out as a factor in the feeding mechanism of this starfish, at least as far as mussels and oysters are concerned.

SUMMARY

The method that *Pisaster ochraceus* uses for feeding on bivalve molluscs cannot be explained in terms of one process. Instead, a number of factors are involved, any one of which, alone or in combination with others, can result in digestion of the bivalve by the starfish. The point of major importance is that this starfish can begin digestion of the soft parts by inserting a portion of its stomach through a small opening in the *closed* shells of mussels and probably most clams. Also important is the apparent lack of sensitivity and response of bivalves to contact with this starfish or its stomach, together with the natural tendency of bivalves to open their shells under water. Voluntary opening may be especially important as far as feeding on oysters is concerned. My work has shown that the idea of pull as an effective factor, originally advanced by Schiemenz (1895-97), is also a valid one. *Pisaster* often uses pull in its feeding process, especially on the smaller mussels, but this is certainly not the whole story. The old problem as to whether a starfish can outpull a bivalve seems to be a relatively unimportant one as far *Pisaster ochraceus* is concerned. Certainly the amount of time that a large bivalve can resist the pull of a starfish becomes reduced in significance if a starfish has already inserted its stomach and initiated digestion within the closed valves. Finally, in contrast with *Asterias forbesi* as studied by Aldrich in an unpublished dissertation, I have been unable to demonstrate that *P. ochraceus* secretes or contains a toxic or narcotic substance useful in feeding on bivalves.

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CORRECTION FOR VARIOUS EXCLUSION ANGLES IN THE RANDOM PAIRS METHOD

A recent article in this journal (Rice and Penfound 1955) indicates that a correction in the use of the random pairs method (Cottam and Curtis 1949) has not been sufficiently emphasized. The paper in which this method was originally presented called for the use of a 160° angle, with computation of mean area based on the formula $(\frac{1}{2}d)^2$ x 3.4644, where d is the average distance between trees. This equation was based on the theoretical assumption of a hexagonal distribution of individuals and can be further simplified to .8661 d^2. Further research on the method (Cottam, Curtis, and Hale 1953) using several different angles of exclusion showed that distance obtained with this method increases as the angle of exclusion is increased, and that this increase is approximately linear over a wide range of angles of exclusion. A 100° angle gives distances equal to the square root of the mean area, while a 180° angle gives distances equal to approximately 125 per cent of the square root of the mean area. These figures, along with figures for several other angles of exclusion are presented in both tabular and graphical form on p. 753 of the 1953 paper. The 160° angle was not used in the research leading to the 1953 paper, but in view of the linear relationship between distance and angle of exclusion, a value can be interpolated from the values given for other larger and smaller angles. Such an interpolation indicates that the 160 degree angle gives distance values equal to approximately 120 per cent of the square root of the mean area. On the basis of this later, more extensive research, computation of mean area and trees per acre when a 160° angle is used should be based on the equations $MA = (d/1.20)^2$ or $(0.83d)^2$, and trees/acre $= 43560 \div (d/1.20^2$. The original equation in the 1949 paper is incorrect and should not be used. The 1953 paper states "any angle throughout this range (0° to 260°) may be used for field work, although angles of exclusion less than 100 degrees yield data with a higher coefficient of variation than do the larger angles. The distances so obtained must be multiplied by the appropriate correction factor to convert them to square root of mean area." In actual practice, a 180° angle is more simple to measure in the field than other angles and for this reason alone is probably the most satisfactory angle to use. The correction factor in the case of this angle is 0.8 and the correction is d x 0.8.

Rice and Penfound do not give the average distance between trees found in their study, but calculation from their trees per acre figure using the equation given in the 1949 paper yields an average distance between trees of 18.1 ft. Application of the correction factor 0.83 produces the following results: square root of mean area, 15.1 ft.; mean area 228 sq. ft., trees per acre, 191.1. The trees per acre figure compares with that of 187.8 for the 100 per cent census made by Rice and Penfound. The error is approximately 2%. Other comparisons of interest in the Rice and Penfound paper are: Average basal area per tree is .277 sq. ft. for the random pairs method and .278 sq. ft. for the census; basal area per acre is 52.9 sq. ft. for the random pairs method and 52.3 sq. ft. for the census. Relative density figures found by Rice and Penfound for the random pairs method show a wide discrepancy from the census figures. Basal areas per tree for two of the species, not given by Rice and Penfound but calculated from their data, are also far from the figures given by the census. These discrepancies may be due, as stated by Rice and Penfound, to the small sample utilized. Only one of the tree species present in this forest was sampled more than 30 times by the random pairs method, and as stated in the 1953 paper of Cottam, Curtis, and Hale, "A minimum of 30 individuals of any species is necessary before any statement can be made regarding its relative density in the population." Another possible explanation is suggested by the presence of compensating errors in the data for hickory. Double the census number of trees per acre were found with an average basal area per tree of only half the census figure. This leads to the suspicion that clumps of small hickories are located in the forest, and these clumps were over-sampled by the random pairs method.

The writers regret that their failure to emphasize the relationship between the results of their 1953 paper and the random pairs paper written in 1949 has led to the continued use of an erroneous equation for the computation of trees per acre with the random pairs method. This note is written to bring to the attention of others the appropriate correction.

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REVIEWS

STRANGE AND MYSTICAL TRANSMIGRATIONS[1]

The "strange and mystical transmigrations" that Sir Thomas Browne observed in silkworms have commanded increasing attention in recent years. Within the past year two distinguished scholars have published important monographs on insect metamorphosis which bring together the diverse and extensive literature; namely, R. E. Snodgrass' "Insect Metamorphosis"[2] and the volume which is the subject of this review, V. B. Wigglesworth's "The Physiology of Insect Metamorphosis." Happily, the approach taken by the two is very different. Snodgrass stresses the comparative morphological aspects of the subject and discusses the degree to which metamorphosis is manifest in diverse insect groups; Wigglesworth focusses on the morphogenetic and physiological aspects of metamorphosis. Both writers relate their findings to questions of interest to the ecologist such as the evolution and origin of metamorphosis, the significance of the pupal stage, the impact of the environment on metamorphosis, etc.

Wigglesworth's monograph like others in this new Cambridge series is brief—40,000 words—and includes a large number of recent findings. Indeed, more than 100 of 337 references are to papers published after 1950. The author uses *Rhodnius*—an hemipteran—as his principal text for physiological thinking about metamorphosis, but he does not neglect other groups. It is rather amusing to note that Snodgrass considers *Rhodnius* to be "essentially ametabolic" an observation which reflects the basically different definitions of metamorphosis now current.

For the ecologist the introduction and the final third of Wigglesworth's monograph are of special interest. In the introduction, the author points out the independence of the life of the larva from the imaginal life that resides latent within it and calls attention to the separate evolution of larval and imaginal stages. "The larva is subject to the influence of its environment, and by the action of natural selection (or whatever other agencies control organic change) it may undergo an evolution of its characters which leaves the adult insect untouched. . . . It follows, therefore, that as soon as there are differences in the mode of life of an adult insect and its larva the characters of the two forms will tend to diverge, and such divergence may reach the extreme that separates the maggot from the fly." This same view is held by Snodgrass who also concurs with Wigglesworth when it comes to questions of the origin of the pupal stage. Both writers subscribe to the Poyarkoff-Hinton theory that the pupal stage arose because "the skeletal muscles require a 'mould' in which the cuticular parts have approximately the same relations as in the adult, and . . . a pupa would become necessary when the anatomical differences are so great that the muscles required by the adult cannot be formed in the larva."

Following the introduction are three thoughful chapters on the histological, endocrinological and biochemical events of metamorphosis including an important section on the quantitative action of the insect hormones which stresses the fundamental role of juvenile hormone of the corpus allatum in controlling the onset of metamorphosis. The effect of environment on metamorphosis is also considered and the author suggests a mechanism whereby the number of moults in an insect may be determined by environmental conditions through an interaction of the central nervous system and the corpus allatum. He cites evidence that the central nervous system "counts the instars" and determines when metamorphosis should occur.

The final chapter on differentiation and polymorphism is both stimulating and puzzling. With great insight the author tackles problems such as the origin of differential growth rates, gene action, the mechanisms of differentiation and determination, regeneration, etc. as they are illuminated by studies of insect development. He then draws his ideas together to support the thesis that "metamorphosis is merely a special case of a general phenomenon which is polymorphism in the widest sense. . . . The diversity of structures formed by the epidermis of the abdomen (of Rhodnius) is an example of polymorphism in every way comparable with polymorphism of different organs of the body or different individuals of a species." This reviewer finds it difficult to grasp this view. In striving for generalization it seems as if the author seeks to explain a little-understood phenomenon—metamorphosis—by homologizing it with a still less-understood phenomenon—polymorphism. However, this is a minor criticism for the book is superbly written and not only worth reading but many parts merit serious reflection. Biologlists in general and students of growth and of insects in particular will find it rewarding. Wigglesworth makes it clear that Sir Thomas Browne was right when he wrote of metamorphosing insects that "Ruder heads stand amazed at those prodigious pieces of Nature, Whales, Elephants, Dromidaries and Camels, . . . but in these narrow Engines there is more curious Mathematicks."

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[1] Wigglesworth, V. B. 1954. The Physiology of Insect Metamorphosis, viii + 152 pp., 45 figs. Cambridge: The University Press. $2.50.

[2] Snodgrass, R. E. 1954. Insect Metamorphosis, iii + 124 pp., 17 figs. Smithsonian Misc. Coll. *122,* No. 9. No charge.

ISLAND BIBLIOGRAPHIES[1]

"The great unsolved problems of scientific methodolgy is that of bibliography, that of knowing what has been accomplished already. In starting any line of investigation the scientist is faced with the choice of ignoring his predecessors, possibly wasting much time on work that has already been done and missing valuable information and ideas or of spending a large proportion of his time in study of current and past literature on the field." With these opening words, the authors make obsolete both their own alternatives by presenting to the scientific public an annotated bibliography of about 5600 entries that is an outstanding landmark of its kind, and one that will enormously simplify future scientific research activities in the pertinent fields.

This publication is an outgrowth of the vegetation studies of the authors in the Pacific region, and is printed under the auspices of the Pacific Science Board of the National Research Council, Washington, D. C. It is essentially three separate bibliographies, each of which had been compiled for different purposes. Arrangement is by author. The references include library call numbers, usually those of the Library of Congress, except where no copy has been seen in a public institution. Annotations briefly describe the contents of the items, and do not aim to abstract them. Early publications on history, travel and exploration, as well as agriculture and economic botany, are exceptionally well combed. Coverage of the Japanese literature is remarkably complete. Many items are included even though they contain little of pertinent value, on the wise but often overlooked thesis that unless included, future investigators would feel obliged to spend time in checking them. Indexes cross-reference the items according to numerous subject headings. Inclusion is up to November 1, 1954, with some items published in 1955.

I. The bibliography of Micronesian botany comprises 103 pages, with 10 pages of addenda and 26 pages of indices. The area covered includes the Marianas, Caroline, Marshall, and Gilbert archipelagoes, besides the isolated islands of Marcus, Wake, Mapia, Nauru and Ocean. In this instance, botany has been construed in its broadest sense, to include anything concerning plants.

II. The bibliography on atolls is an outgrowth of the Coral Atoll program of the Pacific Science Board, and involves in addition to biological science, geography, geology, climate, hydrology, soils and the material culture side of ethnology. It comprises 184 pages, 23 pages of addenda, and 75 pages of indices. The area embraces all tropical seas where atolls occur, principally in the central and western Pacific, but also in the Indian Ocean, the Caribbean and the Gulf of Mexico, and includes Rocas near Brazil, and Clipperton in the eastern Pacific.

III. The selected bibliography of vegetation of the tropical Pacific islands is the most restricted in subject matter of the three, since it deals not with all the natural sciences as of the atolls, and not with all of botany as for Micronesia, but strictly with the vegetation as a complex of plant communities. In this respect it fulfills a unique purpose, for previous botanical bibliographies did not even have "vegetation" as an entry in the indices, and the annotations were not written for the student of plant communities. There are 80 pages, 7 pages of addenda, and an 18-page geographical index.

Those who use this publication may sense certain features of arrangement and organization that are not conducive to calm. The very fact that these three separate bibliographies are published under one title and one cover makes obvious the situation that certain items are repetitiously entered in more than one place. For example, a study of the vegetation of a Micronesian atoll would be entered in all three bibliographies. The regions and the subject matters are not mutually exclusive and overlap in confusing ways, so that the tracing of a known reference can be not only trifold but hexafold, as the three addenda are segregated at the end of the volume. Furthermore, the addenda items are not indexed by subject matter. It is very easy to say that the authors published prematurely, and should have edited the volume into a single coordinated listing. To this charge, I will stoutly defend the authors. I would counterclaim that any shortcomings of this volume are a reflection not of the authors, who are scientists with no assistance from professional bibliographers, and who gave much of their personal time to this production. Rather, it is a reflection of the unwise lethargy of many sciences adequately to finance works of this kind, which are now so urgently needed if new research is to build upon the past. Normal channels of scientific publication tend to limit their activity to what they term "original research," and in doing so, may publish long and costly lists of "Literature Cited," lists that may substantiate or imply the author's worth, yet are often worthless as bibliography, and add nothing to the increase of original knowledge. Whereas these same channels may have an undisguised disinterest in the publication of bibliography, considering it as some inferior type of activity, unworthy of their dignity as purveyors of "original research." In this respect, I am reminded of the lorgnetted garden club lady who affectionately gazes on her "arrangements," but would never never handle the manure that makes them grow, a job which is left for the mere horticulturist. I apologize for the odor of these statements, but I do it in recollection of the correspondence in my files, from the years when I searched in vain for a publisher for my and others' contributions in this field. The tide however is now turning in respect for and appreciation of bibliography. Once in print, bibliographies are used, and more will be wanted. Furthermore, there is a growing realization that the mere gardener who prepares them must be more than mere, that he should be superior, possessing both judgment and discretion, as well as having an infinite capacity for laborious and pains-taking drudgery. Most certainly, these Island Bibliographies will not only be an aid to future scientific research in their fields, but will serve as a noticeable impetus in furthering the entire field of bibliography in the natural sciences.

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[1] Sachet, Marie-Hélène, and F. Raymond Fosberg 1955. Island bibliographies. [I] Micronesian botany. [II] Land environment and ecology of coral atolls. [III] Vegetation of tropical Pacific islands. 577 pages. Washington: National Academy of Sciences—National Research Council Publ. 335. $6.00.

Mumps, Measles and Mosaics[1]

These two recognized British virologists, from the Cambridge group, have preduced a unique little book. It is a book for the amateur naturalist, not for the specialist or the familiar idle reader. No one who gardens or collects wild flowers or mushrooms will be immune to the interest of this book if he has a drop of the experimenter's blood in his veins. For young students in biological science, or for biologists who are expert in a remote field, the book is about as good a general introduction to virology as one can find. It has not the full romance of the epidemiological side, like Burnet's wonderful book, nor of course the solid meat of the advanced Luria text, but it is within its compass a fine book. The emphasis is evolutionary and ecological, with a scope wide enough to include the examples of the title and many more. Vectors, strains, and interaction are stressed; nucleic acid, while its proper importance is recognized, is treated rather lightly, as indeed are all the biochemical and more quantitative aspects of virology. In the light of the fact that of the many references (an excellent attribute for a popular book) nearly all the ones more recent that 1950 refer to phage, this somewhat prejudiced reader felt that the showy and economically important plant viruses got more than their share of attention. Since the authors are genuine authorities in this sub-field, the matter is understandable enough. Indeed, they cannot be praised too much for the chapter on simple techniques of plant virus work, which brings the possibility of amateur virology to every gardener who can grow a few pots of tobacco seedlings under glass. A glossary, a list of tests for common plant viruses, and a useful index complete a book which, with its clear and pleasant style, its authoritative material, and its beautiful pictures, is a first-class example of English popular science. Teachers and school librarians, please note well.

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[1] Smith, K. M. and R. Markham 1954. Mumps, Measles & Mosaics. A Study of Animal and Plant Viruses. 160 pp., 16 plates, 1 color plate. New York: Frederick A. Praeger. $4.00.

The Vegetation of the Coastal Region of Suriname[1]

This excellent work is a book of 135 pages of text plus 32 very good photographs, two vegetation maps in colour, a number of transect profiles and extensive tables of species distribution. The coastal region of Surinam which is described is defined as the area of geologically recent alluvia reaching some 35 kilometres inland from the sea and as this is all very low-lying the vegetation consists largely of swamp and "marsh" (sensu Beard). The field data were collected during an expedition from September 1948 to May 1949. We are promised that Professor Lanjouw is to publish separately on the savannas of the area. Dr. Lindeman has confined himself to the swamp and woody marsh and other communities which actually cover the bulk of the region.

This work must be one of the most important contributions to date on swamp vegetation in the American tropics. Its author complains, perhaps rather justly, that previous workers have tended to avoid swamps in favour of higher land. He himself confesses a liking for the swamp land: "In my eyes the region offers much fine scenery, of which the photographs may give some idea, even though they do not show us anything of the often very fine colour scheme." However, we only have to read as far as p. 31 to find out why other ecologists have failed to share Dr. Lindeman's enthusiasm: they have not shared his hardihood.

> ". . . a zone formed by *brantimakka. Machaerium lunatum,* one of the most dreadful plants to meet with. The very patent branches are criss-cross entangled and the whole shrub is armed from the very base up to the nerves of the leaves with strong, recurved prickles ready to transfix every object that might touch it. Through a small tunnel cut in the *brantimakka* wall we were able to penetrate on hand and foot in one such grove. . . . In the fourth swamp a 4m. high belt of Machaerium scrub had to be tunnelled. The passage was extra disagreeable as this scrub was so old that under it a knee-deep layer of vegetable mud had been accumulated. This mud had the consistency colour and odour of fresh cow dung and appeared to be a characteristic product of the *brantimakka* shrub. The roots and cut-off branches in it gave the foot but a rather tricky hold, and no one reached the other side unscratched."

The vegetation was described and mapped from aerial photographs supported by groundwork involving several transects, one 35 kilometres in length. Soil and vegetation profiles along important sections of these transects have been drawn.

The sea off the Surinam coast is fronted mainly by mangrove and there is little true strand vegetation due to the flat muddy conditions of the shoreline. *Rhizophora mangle* grows in the outer deep water along the rivers but fronting the sea there is mainly Avicennia and Laguncularia. Avicennia may here adopt a pioneer role on accrescent coast, which it has not been reported to do elsewhere. The salinity of the water was repeatedly tested on the transects, and mangrove was found flourishing in all conditions from perfectly fresh water to lagoons which due to evaporation had double the salt content of normal sea water. This observation necessitates some revision of previous conceptions. While it may still be true that brackish conditions are optimum for mangrove, on the one hand it will clearly tolerate open sea conditions in the absence of too much wave motion and given suitable bottom for rooting, and on the other hand will grow in fresh water if not ousted by the competition of other vegetation. The mangroves must be regarded as facultative halophytes. Thickets of *Hibiscus tiliaceus* represent habitats intermediate between mangrove and strand, and those of the *Machaerium lunatum* between mangrove and freshwater swamp.

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[1] Lindeman, J. C. 1953. The vegetation of the coastal region of Suriname. x + 135 pp. Utrecht: Bildiotheck der Riijksuniversiteit.

Semi-Aquatic Swamp is represented by floating meadows of *Leersia hexandra* which are rooted in the bottom but rise up and down with fluctuations in level. Communities of Herbaceous Swamp include a pioneer stage of *Elaeocharis mutata* in brackish water, and associations of *Typha angustifolia-Cyperus articulatus* and *Cyperus giganteus-Typha-Scleria* in fresh to moderately brackish. Two other sedge-dominated communities of radically different and highly interesting character are further included as herbaceous swamp: the one, dominated by *Rhynchospora corymbosa* occurs on beds of thick peat or *pegasse* as it is called in Guiana, and the second, with *Lagenocarpus guianensis,* on a stratum of peat actually floating on the surface of the water. This peat layer varies in thickness from 40 cm. to 2 metres and where thicker may be walked upon with safety. Owing to the quaking nature of their surface these areas were nicknamed swaying swamps.

Woody swamp communities are represented by Arborescent Swamp in the shape of the Machaerium thickets already mentioned, by Swamp Woodland ("Mixed Swamp Wood") and by Swamp Forest, here constituted by an almost pure stand of *Erythrina glauca.* For some reason, this species replaces in Surinam the more usual *Pterocarpus officinalis* which becomes relatively rare.

Marsh vegetation includes a number of forest types. The *Triplaris surinamensis-Bonafousia tetrastachya* type was also described by Fanshawe (1952) from the eastern part of British Guiana where he considered it to be secondary. Its distribution in Surinam suggests that even if this is so, the succession is complete. Fanshawe also recognized the *Symphonia globulifera* type of marsh forest. An unusual assemblage in Surinam is dominated by the deciduous *Hura crepitans* with an understory of characteristic marsh species. Some similarity to this community is to be found locally in and behind the Nariva Swamp in Trinidad. Clearly it is an intermediate between marsh and seasonal forest. Palm Marsh is represented by the *Mauritia-Chrysobalanus* association which is also known in Trinidad and British Guiana. Lindeman considers that this association can occur also as Palm Swamp.

Forests of the higher ground consist mainly of Evergreen Seasonal Forest of types recognized also by Fanshawe, and of "Savanna Forest" which is in general the "Marsh Woodland" of Beard, though it is rather a wide term and includes a range of communities. The name Savanna Forest was evidently chosen because very often these communities stand in close relationship to savannas and exhibit a range of gradations from savanna to high forest. They hardly, however, conform to a Schimperian definition of savanna forest. Sometimes, on white sand ridges, the "Savanna Forest" is properly Dry Evergreen Woodland or Thicket.

Some difficulty was admitted in sorting out the ecological relationships of swamp communities. In general there does appear to be a developmental sequence from the floating Leersia through the various herbaceous types to swamp forest as Beard has suggested, but it is not just a simple expression of the depth of water. The Leersia type is evidently one of somewhat deep water, or at least of water of fluctuating level which may become deep, and the other herbaceous communities are determined by water depth to some extent. It is found, however that the Erythrina forest occupies deeper water than the surrounding herbaceous vegetation. Salinity must also be taken into consideration, as well as the nature of the rooting medium and the aeration of the water. Leersia was found in water of very varying salt content but among the herbaceous swamp types proper there were found to be associations more or less representative of salinity differences from Elaeocharis in brackish water to *Cyperus giganteus* in fresh. The degree to which the water has become stagnant and deprived of oxygen was not considered by Lindeman but must certainly be a most important factor in these communities. The oxygen content of the ground water would probably be somewhat difficult to measure and would have to be inferred from reducing capacity, or other test of an indirect nature. It is suggested that this factor may be found to explain a number of the apparent anomalies in swamp community distribution. Swamp Forest and Woodland for example may be found associated with creeks, drainage channels and lines of moving water which imply a better aeration. It is observed that there is no peat under *Erythrina glauca.* If this tree represents areas of better aerated water peat would not form, or if it had done so previously would waste under the improved conditions. For peat formation conditions must be anaerobic.

To lay stress upon the importance of stagnant ground water serves to clarify also some of the more obscure points of difference between marsh and swamp. In Beard's paper of 1944 an attempt was made to define the relationships of these two quite distinct groups of edaphic formations and it was suggested that a swamp habitat is perpetually moist, ranging from inundated to just moist but never desiccated, at least not for effective periods, whereas a marsh habitat is seasonally waterlogged, seasonally desiccated. The cause of this severe alternation in marsh soils is impeded drainage, due to pan or impermeable subsoil or high watertable with no outlet, whereas a swamp soil would be freely draining. Such a simple distinction serves readily enough to characterise the savanna habitat and to separate it from other communities, but it is rather too simplified to be quite sound in the case of woody types of marsh. Even in the case of savanna, Lindeman falls into the error of placing a wrong emphasis, as on p. 82: "the periodical complete dryness is the essential factor for the savannas and inundation in the rainy season is not obligate." In fact, exactly the opposite is the case: to produce savanna it is essential that a site be if not actually inundated at least waterlogged in the rainy season and there are savannas that never become completely dry. Seasonal dryness on well-drained soil gives one seasonal forest, thorn woodland or cactus scrub. On badly drained soil it gives savanna because here we have the concomitant factor of water-logging during the rainy season. For the reason that the savanna site must be flat, with drainage impedance and, usually, a perched watertable, the rain water cannot drain away but lies in pools and in the soil until it slowly percolates laterally or is evaporated in the next dry season. During this time it becomes stagnant and deficient in oxygen.

The drainage regime of woody marsh vegetation is similar, but here the waterlogging factor is predominant and the seasonal desiccation may or may not be actually present. For all marsh there must be impeded drainage but too much emphasis has been placed on the necessity for a seasonal alternation of moisture in the case of the woody formations. These only occur in high rainfall areas and often on such sites as the pegasse soils of

Guiana which as we now know can scarcely be said to become very dry in the dry season. Essentially, it is clear, the drainage impedance and waterlogging imply the presence of stagnant ground water. It is felt that this is likely to be the essential factor which differentiates marsh from swamp. In swamp the ground water is replenished from rivers, kept moving by tidal action or lateral drainage, or otherwise kept relatively well aerated. In marsh the groundwater is stationary and becomes stagnant.

This distinction will serve also to clarify the position of the Rhynchospora and Lagenocarpus communities of the "Swaying Swamp" habitat, which were classified by Lindeman as herbaceous swamp but which are correctly speaking sedge savannas. He commented himself on the close floristic relationship between them and the Aripo Savannas in Trinidad where there is no peat and where it is obvious that a savanna type of habitat is present. Close affinities to savanna could be remarked even in Surinam, viz:

"Between these two islands the swamp was about 2m. deep while the peat layer was only 40-50 cm. thick and very loose. This made it difficult to move over . . . however, our efforts were richly rewarded because we detected here a real floating savanna, complete even with the small shrubs, a thing we had never heard of."

Sedge savannas of this floristic type are not uncommon in the wetter parts of the tropical America and represent the extremest, most strongly inundated and badly aerated marsh habitat without effective seasonal desiccation. Elsewhere, they are clearly marsh and a type of savanna. The swaying swamps of Surinam are so far the only case where this floating peat has been reported and where the habitat might readily be assessed as swamp if no enquiry were made into the aeration of the ground water. It is fairly clear that there must be anaerobic conditions in the Swaying Swamp for the peat to have accumulated in the way it has. In the same way the Mauritia-Chrysobalanus association bordering the swaying swamps and sometimes other swamps and swamp forest is marsh vegetation, less strongly inundated than the sedge savanna, but like it in stagnant groundwater.

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THE DANCING BEES[1]

Here is a book that will give a good picture of the experimental study of animal behavior to the general reader and amateur naturalist by one of the newest and most successful contributors to the great store of knowledge and long list of books about bees. It is based upon forty years of research on the senses and behavior of the honey-bee by Professor von Frish, entomologist of the University of Munich. It attempts to give the interesting facts, fascinating and amazing as they are, without too many technical details and without wandering into "poetic fancy" as some of the classic older books do.

The first section of the book deals with general information about the structure and life-history of the honey-bee. It tells how the bees construct the hive, collect nectar and pollen, rear the brood, control the sex of the offspring and carry on all the complex activities of the beehive. Interesting bits, told with straightforward simplicity, refer to the geometrical superiority of hexagonal cells in the comb, regulating hive temperature to an optimum ninety-five degrees and the unbelievable activity required to produce a thimbleful of honey. As many as ninety thousand visits to individual florets may be made. Nevertheless, in a good season an active colony may store two pounds of honey per day. In such a colony more than a thousand workers hatch daily and as many may die in one day from "old age" and accidents.

The most interesting part of the book deals with the author's well known and important observations on the sensory perception and "language" of the bees. Using simple but cleverly designed field tests he has proved that honey-bees can distinguish colors, tastes, shapes and polarized light. The description of his theory of the perception of polarized light by the compound eyes of the bee and its use in orientation is a highlight of this book and of all modern studies of insect behavior.

The "language" of the bees consists of certain gyrations called "dances" which are performed by foraging workers upon returning to the hive. "Round Dances" and "Wagging Dances" are recognized which, together with scent, inform other workers in the hive of the amount, kind, distance and even direction of the nectar sources. It is not only fascinating but very provocative reading to become aware of such complex and directed behavior on the part of an insect. The last two chapters introduce the reader to the possibilities of studying other and equally interesting forms of social organization among bumble-bees, wasps and ants. The author is indebted to Dora Ilse for a fine translation preserving his simple, facile style and making it good reading in English.

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[1] Von Frisch, K. 1955. The Dancing Bees. xiv + 183 pp., 61 figs., 30 plates. New York: Harcourt, Brace and Company. $4.00.

THE FORESTS OF CUBA[1]

This book is the outcome of a project by a student from the United States to report on the forest resources of Cuba, but in addition to the forest inventory it contains much matter of ecological interest. In such a study forest types must be recognized and classified and some details given of their environment. The first chapter is an introductory and describes *inter alia* the location of the few remaining forest stands in Cuba and their exploitation. The second chapter devotes five pages to a description of the Factors of the Environment—Geological Patterns, Climatic Patterns and Land Use Patterns—giving a concise summary of these necessary ecological data. Chapter III, Vegetation, contains an attempt to classify the forest types, which are described in detail in Chapter IV. The latter comprises 60% of the whole book. A final chapter deals with the apparent relationship between the forest types and the factors of the environment. The numerous photographic illustrations are of very high quality.

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[1] Smith, E. E. 1954. The forests of Cuba, viii + 98 pp., 36 plates, 2 maps. Maria Moors Cabot Foundation. Pub. No. 2.

In classifying the vegetation the author reviews previous descriptions of the plant communities of the island, none of which he feels have provided a satisfactory basis of classification. Thus Seifriz[2] presents a classification which "consists of geographic, geologic, edaphic, climatic and vegetational aspects listed without rank or order." Much the same applies to Carabia.[3] The more general systems suggested for the American tropics by Barbour[4] and Beard[5] are also discussed and likewise discarded, seemingly for the reason that they were too difficult to apply. One rather gets the impression that the author was bewildered by the complex vegetation patterns in Cuba and found their reduction to order somewhat baffling. It is certainly possible to sympathise with him: to attempt to grapple successfully with the subject on the basis of two brief preliminary visits and a year's field work, after no other experience of the tropics, is no mean task, particularly in Cuba where the occurrence of pines adds at first sight even greater confusion to the ecological assemblage. However, since the Beard system has been successfully applied to the neighbouring island of Jamaica by Asprey and Robbins[6], there seems no reason why it should not also be used in Cuba, once the principles are well enough understood.

Two examples are given by the author to illustrate the inapplicability of the Beard system, and both also illustrate his own sense of frustration. In the Baracoa region of eastern Cuba he records that he was constantly confronted with a variety of types and complains it is exceedingly difficult to tell which types have reached a climax and which will yet reach it in sufficient time. This region, he says, is often considered to be a true rain forest, but is found to consist of a mass of sharp ridges supporting a comparatively dry forest called locally *monte bravo* and varying in form and composition from the *monte fresco* of the valley floors. Other tropical experience would have shown the author that this catenary arrangement is quite usual and fits quite harmoniously into the framework of seasonal forests. The *monte fresco,* "luxuriant *Carapa* type forest of the valley floors" is clearly Evergreen Seasonal Forest, while the *monte bravo* is Semi-Evergreen Seasonal Forest in the Beard system. Worrying about which of these is the true climax is beside the point. This was fully discussed by Beard[7] in 1946, pp. 142 et seq.

Secondly, the author admits a severe problem in distinguishing between evergreen and deciduous stands during the wet season when these characters are not apparent. This can but strike one as *naïve.* Surely one does not suppose that classification of a stand is made by actual species counts of leafless trees during the dry season? In actuality, the obligately and facultatively deciduous species are picked out from the species list from general knowledge of their behaviour, which may be obtained from reference works or by consulting the locals.

The author's own classification of the forest types of Cuba is purely silvicultural: primarily into Forests, Grasslands, Desert Scrub and Cultivated Areas and Pastures and secondarily a division of the forests into Pine and Broadleaf, these being further broken down by soil types. For forest inventory purposes, a major distinction between pine and broadleaf forests would be a necessity, but ecologically the separation is at a lower level. The genus Pinus is not generally present in tropical America, occurring only in the Bahamas, Hispaniola, Cuba and neighbouring parts of Central America. It is an alien invader from the temperate zone and has established itself by means of its wide tolerance of inhospitable conditions in certain niches where the native tropical vegetation is depauperate and does not offer effective competition. Pine is absent from communities of luxuriant growth, but it has entered a number of quite unrelated scrub and grassland communities and given them a superficial unit which in fact they do not possess. Hitherto, ecological views of these communities have tended to be dominated by this superficial unity but although Earl Smith's work also follows this pattern, the details he gives us are indeed illuminating of the true state of affairs and throw a great deal of light on a previously obscure and confusing subject.

Pine forests are said to occur in three habitats:

1. Small areas in the Sierra Maestra in Oriente Province.
2. "Lateritic" soils derived from serpentine in eastern Oriente and in Pinar del Rio.
3. Shales and interbedded sandstones, and sandy areas in Pinar del Rio and the Isle of Pines.

Pine may be present also in savannas under the category of grassland.

In the Sierra Maestra the pine is *Pinus occidentalis.* It occurs mainly in the 3,000-5,000 ft. altitude belt, on dry ridges, small relatively dry knolls, steep rocky slopes, steep slopes of southern exposure, landslide areas and the amphitheatre-like ravine heads where mineral soil is exposed, wherever, in fact, the associated vegetation does not offer serious competition to a hardy species. In some of these sites the pine is obviously a pioneer which will be succeeded by broadleaved forest and its rank is seral. Elsewhere it is by way of forming an edaphic climax.

On the red earth derived from serpentine we find *Pinus cubensis* in Oriente and *P. caribaea* in Pinar del Rio, sharply confined to these soils, with belts of hardwoods along watercourses. Apparently broadleaved species can also form forest on serpentine if the soil is not deep, but there will be pure pine stands on deep soil. This the author attributes to the excessive porosity of these soils and lack of moisture retention. If this is the case it is not clear why we do not find drier seasonal or dry-evergreen communities composed of broadleaved species, such as occur on the limestone *mogotes* or areas of low rainfall. One is not convinced that the author has got to the bottom of the matter here. The operation of some chemical factor such as nickel toxicity needs to be investigated. In either case the pine forest must rank as some kind of edaphic climax. Alternatively, perhaps the Dry Evergreen Forest dominated by Calophyllum which now occurs at higher elevations on the serpentine was formerly more extensive and was destroyed by fire.

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[2] Seifriz, W. 1943. The Plant Life of Cuba. Ecol. Monog. 13; 375-426.

[3] Carabia, J. P. 1945. A Brief Review of the Cuban Flora. Plants and Plant Science in Latin America.

[4] Barbour, W. R. 1942. Forest Types of Tropical America. Carib. Forester 3; 137-150.

[5] Beard, J. S. 1944. Climax Vegetation in Tropical America. Ecology 25; 127-58.

[6] Asprey, G. F. and Robbins, R. G. The Vegetation of Jamaica. Ecol. Monog. 23; 359-412.

[7] Beard, J. S. 1946. The Natural Vegetation of Trinidad. Oxford Forestry Memoir 19.

The third habitat is on the shales and sandstones of the San Cayetano formation, where two pine species occur together, *P. tropicalis* and *P. caribaea,* occupying the low rounded ridges which lie between small ravines or larger valleys. The ridges are described as of very thin soil or rapidly weathering rock. Again it is not clear why we do not have a broadleaved scrub. Possibly there is seasonal waterlogging on these sites, bringing them into the category of savanna soils: possibly, on the other hand, fire has been responsible for eliminating or suppressing hardwoods. The role of fire is nowhere discussed in the book.

In the last two habitat groups, the ecological factors associated with occurrence of pine do not appear to have been entirely satisfactorily accounted for, although our information has been materially increased.

J. S. BEARD

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